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Studies on the Taxonomy, Morphology, and Biology of Prosthogonimus Macrorchis Macy, A Common Oviduct Fluke of Domestic Fowls in North America

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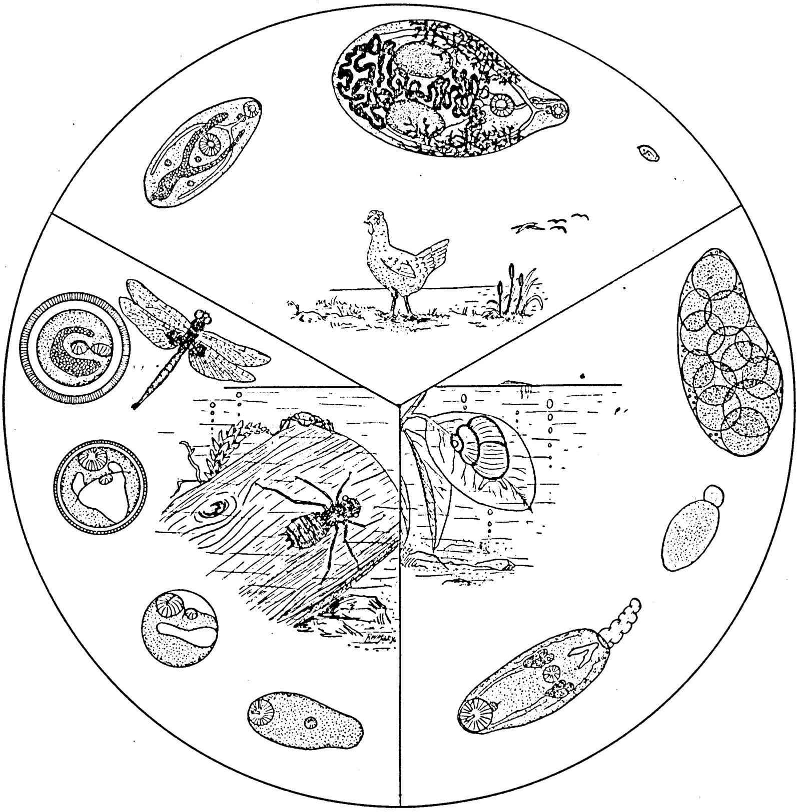

Life Cycle of the Oviduct Fluke From Hen to Snail, to Dragonfly Naiads, and Back to Fowls Which Feed on These Insects

ACKNOWLEDGMENTS

Special acknowledgment for aid in the course of this work and for making possible its completion is due Dr. W. A. Riley and Dr. D. E. Minnich, Chairman of the University Department of Zoology. Many others have contributed. To Dr. F. B. Hutt and his staff I offer my sincere thanks for their hearty co-operation. Others who have aided me materially are Drs. A. R. Ringoen, R. L. Donovan, A. A. Granovsky, M. N. Levine, Miss Ethel Slider, and Messrs. Gustav Swanson and W. W. Crawford. My wife, also, has helped at all times, but especially with mollusc collections and dissections. I am likewise very grateful to Dr. James G. Needham of Cornell University for checking the identification of the important dragonfly hosts, and to Dr. Frank C. Baker of the University of Illinois for similar help with the snail host.

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STUDIES ON THE TAXONOMY, MORPHOLOGY, AND BIOLOGY OF *PROSTHOGONIMUS MACRORCHIS* MACY, A COMMON OVIDUCT FLUKE OF DOMESTIC FOWLS IN NORTH AMERICA[1]

RALPH W. MACY

INTRODUCTION

For many years farmers and poultrymen in the lake regions of Minnesota have noted a sharp decline in egg production in early summer. The few eggs that were produced were often soft-shelled and otherwise malformed. There was a large mortality of adult hens during this season, particularly of birds having free access to swampy ground and to shores of lakes with much vegetation. A few keen observers among the farmers have advanced the idea that this was the result of the hens feeding on "bugs" which they picked up along the shore.

That this suspicion was well founded has been amply demonstrated by work conducted during the last few years by various members of the division of entomology and economic zoology of the University of Minnesota. The so-called "bugs" are the immature stages, or naiads, of certain swift-flying dragonflies, or "mosquito-hawks," which emerge from the water in enormous numbers at the season when the trouble is most pronounced. As will appear in the historical discussion, these insects have been implicated by the work of certain European investigators and by that of Kotlan and Chandler in this country.

The insect is not the direct cause of the trouble but is the carrier of an encysted fluke, or trematode parasite, which matures in the oviduct and bursa Fabricii of the domestic hen and of ducks. Herein are presented the results of investigations made by the writer on the taxonomy, geographical distribution, morphology, biology, and economic importance of *Prosthogonimus macrorchis* Macy, 1934, the trematode that is chiefly concerned in North America. Altho seen by Linton, 1887, from a hen's egg from Wisconsin, and studied by Kotlan and Chandler, 1925 and 1927, and by Lakela, 1931, its identity as a species separate from European members of the genus was not established until 1934.

The present investigation, a co-operative project of the department of zoology and the division of entomology of the University of Min-

[1] The investigation herein reported is a co-operative project of the Department of Zoology and of the Division of Entomology and Economic Zoology of the University of Minnesota, carried out under the direction of Dr. W. A. Riley.

nesota, was carried on in the vicinity of Minneapolis, Minnesota, in a region of numerous lakes. Fortunately, one nearby lake, Glenwood Lake, contained dragonfly naiads heavily infested with *Prosthogonimus* cysts. Lake Johanna, not far distant, offered the convenience of uninfested naiads for experimental purposes.

GENERAL METHODS AND TECHNIC

At the beginning of the work, a general survey was made of the fauna of the lakes in the region of Minneapolis to determine especially the nature of the dragonfly and mollusc populations, and to obtain data relative to the prevalence of *Prosthogonimus* cysts in the dragonflies of the various habitats.

Adult dragonflies were captured in quantities on damp days or early mornings by sweeping vegetation near the lake-shore. Naiads were readily obtained by means of the Needham aquatic rake drawn over the bottom, bringing with it naiads from both the substratum and the vegetation. At the time of general spring emergence, when most of the dragonfly naiads concentrate along the shore, one can collect large numbers with little effort.

Molluscs were collected from vegetation obtained by the Needham rake or by hand-picking from submerged plants and sticks.

In the laboratory, specimens were kept in wide, shallow vessels in order that maximum oxygen consumption might be induced. The snails were fed on bits of tender lettuce which they readily ate. From five to ten dragonfly naiads were kept in each of a large series of finger bowls. In a cool place, naiads of *Tetragoneuria, Leucorrhinia,* and *Epicordulia* lived for two months or more without having to be fed, but experimental animals were provided with food once or twice a week to insure best results. By far the most acceptable food was found to be small gammarid crustaceans. Large *Gammarus* occur in great quantities in the small, swift streams and these formed the bulk of the food given to the dragonflies. Smaller naiads readily ate *Hyallela,* plancton crustaceans, and small worms. Attempts to use damsel-naiads as food were not successful.

The large cysts of *Prosthogonimus* were easily obtained by tearing to pieces the dragonfly abdomens under water and were then fed to experimental birds. To obtain metacercaria from the mature cysts, the latter were placed first in dilute HCl and pepsin and then in an alkaline solution of trypsin, in trypsin only, and even in water made alkaline with sodium carbonate.

To obtain eggs from the flukes, living specimens were placed in cold water, following the procedure of Krull, 1931. As they relaxed, the eggs poured from the genital pore in long masses. Adult flukes were killed in corrosive-acetic fixative, in the extended condition, and were stained in borax carmine or Ehrlich's acid haematoxylin.

A method was developed for making permanent mounts of the minute sporocysts and cercaria whereby a large percentage of the specimens could be saved. With a fine medicine-dropper pipette some of these small forms were placed on a slide previously smeared with egg-albumen fixative, and the excess water was then removed. A drop of 70 per cent alcohol was allowed to fall upon the specimens, affixing them to the surface film so that the slide with its adhering material could now be stained and dehydrated by the methods regularly employed with sections. Young metacercaria were treated in the same manner when permanent mounts were desired.

Instructive balsam mounts of whole labia, coxae, and entire abdomens of infested naiads were made by killing the insects in corrosive sublimate, clearing in synthetic oil of wintergreen, and placing in round, balsam-filled cells. These were fashioned from strips of passe partout binding fastened to slides by means of glass-mending cement.

Of several stains tried, Dominici's stain (eosin-orange G and toluidin blue) yielded the best results for detecting leucocytes in sections of hen oviducts infested with *Prosthogonimus*.

TAXONOMY

Hanow, 1753 (also 1749, according to de Blieck and van Heelsbergen, 1923), found in a freshly laid hen's egg two specimens of a fluke which is now known as *Prosthogonimus ovatus*. Lühe, 1899, established the genus *Prosthogonimus*, designating Rudolphi's *ovatus* as the type. At the present time a total of 16 species of the genus is known, and these are found in Europe, Asia, Africa, and North and South America.

Since the specimens of *Prosthogonimus* found in our studies clearly represented a new species, the writer (1934) described it as *P. macrorchis*. For convenience, the specific diagnosis is repeated, and there is added a key for the separation of the 16 known species of the genus, a discussion of the taxonomic position of the genus, a summary of the descriptions of the species of the group, and a review of the specific characters used.

Prosthogonimus macrorchis Macy, 1934
(Plate I, Fig. 1)

1887 *P. ovatus,* Linton, Proc. U. S. Nat. Mus. 10:367.
1925 *P. pellucidus* (?), Kotlan and Chandler, Jr. Am. Med. Vet. Ass. 67:756.
1931 *P. pellucidus* (?), Lakela, Poult. Science, 11:181.
1931 *P. pellucidus,* Shen, Bull. Soc. Zool. Fr., 56:468.

Prosthogonimus: Body pyriform, 7.56 mm.[2] long by 5.26 mm. wide. Cuticula heavily spined cephalad, less so caudad. Oral sucker 0.49 mm. long by 0.56 mm. wide. Pharynx 23 µ long by 22 µ wide. Oesophagus 0.16 mm. long. Intestinal ceca nearly reaching posterior end of body. Ventral sucker 0.92 mm. long by 0.85 mm. wide; anterior edge situated 1.56 mm. from the anterior end of body.

Testes 1.66-1.78 mm. long by 1.65 mm. wide, situated at the junction of the posterior and middle thirds of the body length. Cirrus sac nearly straight; 0.2 mm. wide; base located 1.1 mm. from the anterior end of the body, ending at the level of the intestinal fork. Seminal vesicle much coiled.

Ovary 0.85 mm. long by 1.1 mm. wide, consisting of about 15 closely clustered lobes; situated immediately posterior to the ventral sucker. Seminal receptacle present at the mid-posterior edge of the ovary. Vitellaria begin at the level of the ventral sucker and end at or before the posterior margins of the testes; arranged in 8-9 lateral clusters, follicles large and more or less broadly connected. Uterus with a centro-dorsal descending limb and a more extensive ascending part; no pre-acetabular, heavy coils. Anterior two-thirds of uterine field only slightly wider than the inter-testicular zone but posterior third expanded to lateral edges of body. Eggs average 0.028 mm. long by 0.016 mm. wide; posterior spine variable in shape and length.

Type host: reared in the domestic hen, *Gallus domesticus.*

Habitat: oviduct and bursa Fabricii.

Locality: Minneapolis, Minnesota.

Type: U.S.N.M. Helm. Coll.; paratypes: University of Minnesota Helm. Coll; author's collection.

Table 1

Measurements of *P. macrorchis* from Oviduct of Hen

	Type	Cotype 2	Cotype 3	Cotype 4
Body length (mm.)	7.56	8.5	6.3	7.3
Body width	5.26	5.1	6.0	5.2
Oral sucker, length	0.49	0.486	0.486	0.486
Oral sucker, width	0.52	0.504	0.486	0.468
Ventral sucker, length	0.92	0.774	0.666	0.630
Ventral sucker, width	0.85	0.882	0.792	0.792
Pharynx, length	0.23	0.216	0.216	0.234
Pharynx, width	0.22	0.216	0.198	0.216
Cirrus sac, length	1.1	0.900	0.900	0.900
Testes, length	1.66–1.78	1.780–1.772	1.764–1.782	1.980–1.620
Testes, width	1.35–1.62	1.530–1.440	1.296–1.368	1.080–1.332
Ovary, length	0.85	1.044	0.720	0.882
Ovary, width	1.1	0.935	1.494	1.530

[2] Measurements are of the type.

Differentiation

P. macrorchis belongs to the subgenus *Macrogenotrema* Skrjabin and Baskakow, 1925, (see Skrjabin and Massino, 1925), since (1) the vitellaria consist of coarse follicles arranged in definite groups, and since (2) heavy uterine coils are not found anterior to the acetabulum, as in the case of *P. ovatus*.

Our species may be distinguished from all of the others of the genus by the following combination of characters: Ventral sucker at least a half larger than the oral sucker, ovary definitely posterior to ventral sucker, cirrus sac never approaching the ventral sucker, testes very large (in oviduct specimens) and far posterior to the ovary, and vitelline glands begin at level of ventral sucker but do not extend posterior to testes. *P. macrorchis* superficially resembles *P. pellucidus* (von Linstow), but is distinguished from that species by the fact that the suckers of *P. pellucidus* are sub-equal, while in the former the ventral sucker is considerably the larger of the two. A comparison of the suckers of the 16 paratypes shows that the oral sucker has an average diameter of 0.48 mm. and that the ventral sucker averages 0.761 mm. in diameter, or more than one-half larger. There is little deviation from the ratio of 1:1.56 shown by the entire series, indicating the value of this character for our immediate purpose. O. von Linstow, 1873, states that the ratio of oral and ventral suckers of *P. pellucidus* is as 1:1.3. Braun, 1902, lists a number of measurements of the suckers of this species, which average 0.749 mm. for the oral sucker and 0.916 mm. for the ventral sucker, or 1:1.22. Szidat, 1921, in his description of *P. intercalandus* (synonym of *P. pellucidus*), gives the diameter of the oral sucker as 0.46 mm. and that of the ventral sucker as 0.5 mm. or 1:1.08. On the basis of existing descriptions it may be concluded that there is a definite ratio difference between the suckers of the two species.

The distribution of vitellaria is also different in the two species. In *P. macrorchis* the vitellaria begin at the level of the ventral sucker and do not extend posterior to the testes except in rare cases, as in some very young specimens or in excessively flattened material in which the testes are displaced.

The 16 valid species of the genus *Prosthogonimus,* including *P. macrorchis,* may be separated by the following key:

1. Suckers approximately the same size 2
   Ventral sucker at least a half larger than the oral sucker 4
2. Cirrus pouch not extending posterior to level of intestinal bifurcation 3
   Cirrus pouch reaching nearly to acetabulum ....
   ....*P. furcifer* Railliet, 1924

3. Cirrus pouch very sinuous. Anterior margin of vitellaria considerably behind level of posterior margin of ventral sucker ....*P. japonicus* Braun, 1901
   Cirrus pouch not sinuous. Vitellaria begin at the level of the ventral sucker ....*P. pellucidus* (von Linstow, 1873)
4. Ovary dorsal to the ventral sucker or at least considerably overlapping it 5
   Ovary definitely posterior to ventral sucker 7
5. Uterus with heavy pre-acetabular coils. Vitellaria not confined to anterior half of body 6
   No heavy pre-acetabular coils of the uterus. Vitelline glands confined to anterior half of body ....*P. vitellatus* Nicoll, 1915
6. Vitellaria extending much posterior to testes ....*P. ovatus* (Rudolphi, 1803)
   Vitelline glands not reaching posterior margin of testes ....*P. dogiele* Skrjabin, 1914
7. Cirrus pouch not reaching ventral sucker 9
   Cirrus pouch reaching ventral sucker 8
8. Ventral sucker situated immediately after intestinal fork ....*P. brauni* Skrjabin, 1919
   Ventral sucker located at some distance posterior to intestinal fork ....*P. putschkowskii* Skrjabin, 1913
9. Testes situated at level of ovary 10
   Testes post-ovarial 11
10. Uterus entirely inter-cecal. Cirrus pouch extending far posterior to intestinal fork. Vitellaria separated into distinct follicular groups ....*P. skrjabini* Zakharow, 1920
    Cirrus pouch reaching only to intestinal fork. Vitellaria massed. Very small species ....*P. karausiaki* Layman, 1926
11. Vitellaria beginning at level of ventral sucker 13
    Anterior border of vitellaria definitely post-acetabular 12
12. Testes located at the middle of the longitudinal body axis. ....*P. anatinus* Markow, 1902
    Testes between the first and middle thirds of the body length ....*P. horiuchii* Morishita and Tsuchimochi, 1925
13. Vitellaria extending much posterior to the testes 14
    Vitellaria ending at or before the posterior margins of the testes ....*P. macrorchis* Macy, 1934
14. Uterine coils extending laterally over the intestinal ceca and filling most of the posterior half of the body 15
    Coils of the uterus not reaching lateral portions of the body; entirely inter-cecal ....*P. rudolphii* Skrjabin, 1919

15. Ratio between oral and ventral suckers as 1 :3. Cirrus pouch very sinuous ....*P. fuelleborni,* Skrjabin and Massino, 1925
Ratio between oral and ventral suckers as 1 :2. Cirrus pouch nearly straight ....*P. cuneatus* (Rudolphi, 1809)

Taxonomic Position of the Genus *Prosthogonimus*

Travassos, 1928, followed by Lucker, 1931, in his revision of the family Plagiorchiidae, lists the family Prosthogoniminae as one of the six sub-families. Previously, Nicoll, 1915, without any characterization created the family Cephalogonimidae, which was evidently intended to include the subfamily Cephalogoniminae. Poche, 1926, stated that in these groups Nicoll included only the genus *Prosthogonimus* and the new species, *P. vitellatus,* his list being a purely faunistic one in which other species belonging to this family were not encountered. Poche placed in the family Cephalogonimidae the genera *Cephalogonimus* Poirier and *Emoleptalea* Looss, and he further excluded the genus *Prosthogonimus* and added it to the family Plagiorchiidae. As it now stands, the genus *Prosthogonimus* is considered a member of the subfamily Prosthogoniminae of the family Plagiorchiidae.

Stiles, 1901, pointed out that on the basis of priority of publication of one day, the generic name *Prosthogonimus* Lühe, 1899, is to be accepted rather than *Prymnopryon* Looss, 1899. Lühe, 1909, included in his subfamily Prosthogoniminae the two genera *Prosthogonimus* and *Schistogonimus,* the latter having been erected by him at the time for *S. rarus* (Braun, 1901). In the genus *Schistogonimus,* the male and female genital openings are some distance apart and the uterus is centralized and intercecal, while in the case of *Prosthogonimus* the genital pores are very close together and the uterus is, in general, not confined to the central area of the body but extends to the lateral edges. The former character appears to some extent in *P. rudolphii* and in *P. skrjabini.*

The species of the genus *Prosthogonimus* have been reviewed by Braun, 1901 and 1902, Skrjabin, 1913, and Shen, 1931. A brief summary, including all essential points, is given here in order that identification of the members of the group may be made with a minimum of difficulty.

Genus *Prosthogonimus* Lühe, 1899
Syn., *Prymnopryon* Looss, 1899
P. ovatus (Rudolphi, 1803)
(Plate II, Fig. 4)

Alessandrini, 1929; Braun, 1900, 1901a, and 1901b; Cobbald, 1861; von Linstow, 1878; Linton, 1887, Looss, 1899; Lühe, 1899, 1909; Neumann, 1909; Neveu-Lemaire, 1912; Perroncito, 1901; Rudolphi, 1809;

Skrjabin, 1913, 1928; Skrjabin and Baskakow, 1925; Skrjabin and Baskakow, 1925, Sonsino, 1890; Sprehn, 1932; Theobald, 1896; Travassos, 1928.

Description: Body length 3-6 mm., width 1-2 mm. Oral sucker 0.146-0.167 mm. long by 0.167-0.208 mm. wide. Ventral sucker 0.396 mm. long by 0.354-0.447 mm. wide, located some distance from intestinal fork. Vitellaria always begin anterior to ventral sucker and end at level of middle of testes. Uterine coils fill region between intestinal fork and ventral sucker. Eggs 0.022-0.024 mm. long by 0.013 mm. broad.

Hosts: Intestine: *Anas anser;* bursa Fabricii: *A. clypeata, A. ferina, A. glacialis, A. marila, A. musica, Ardea grus, Colymbus griseigens, Corvus cornix, C. frugilegus, C. pica, Falco buteo, F. nisus, F. subbuteo, Fringilla coelebs, F. montana, Fulica atra, Gallinula choropus, G. porcana, Garrulus brandti, Lanius minor, Larus canus, Numenius arcuatus, Nyroca hyemalis, Ortygometra porzana, Otis tarda, Pica caudata, Podiceps subcristatus, Scolopax gallinago, S. rustica, Stercorarius parasiticus, Strix brachyotus, Turdus viscivorus, Uria grylle, Vanellus cristatus, Harpiprion cayennensis, Piaya cayana, Molybdophanes caerulescens, Xiphorhynchos dorbigniana, Monasa nigrifrons, Cyanocorax cyanomelas,* and *Gallus domesticus;* oviduct: *Phasianus gallus;* egg: *Gallus domesticus.*

Geographical distribution: Europe, Northern Asia, and South America.

P. cuneatus (Rud., 1809)
(Plate II, Fig. 5)

Alessandrini, 1929; Braun, 1901a, 1901b, 1902; Creplin, 1846; von Linstow, 1873; Looss, 1899; Lühe, 1909; Neumann, 1909; Neveu-Lemaire, 1912; Railliet, 1895; Skrjabin, 1913, 1923, 1928; Skrjabin and Massino, 1925; Sprehn, 1932; Theobald, 1896; Wedl, 1858.

Description: Body length 5.2 mm., width 1.7 mm. Oral sucker 0.3-0.4 mm. in diameter. Ventral sucker 0.6-0.8 mm. in diameter, located some distance back of intestinal fork. Cirrus sac sinuous, reaching to intestinal fork. Vitellaria reaching from ventral sucker to a position somewhat posterior to testes. Heavy uterine coils not filling region between intestinal fork and ventral sucker. Eggs: 0.0228-0.0273 mm. long by 0.013 mm. wide.

Hosts: bursa Fabricii: *Ardea cinerea, Casarca casarca, Colymbus nigricans, Corvus cornix, C. corone, Cygnus cygnus, Fulica atra, Garrulus glandarius, Grus cinerea, Nettion crecca, Nyroca clangus, Passer domesticus;* egg: *Gallus domesticus.*

Geographical distribution: Europe and Northern Asia.

P. pellucidus (von Linstow, 1873)
(Plate II, Fig. 1)

Alessandrini, 1929; Braun, 1901a, 1901b, 1902; Hieronymi and Szidat, 1921; Lühe, 1909; Neumann, 1909; Neveu-Lemaire, 1912; Ono, 1931; Shen, 1931; Skrjabin, 1923; Szidat, 1926 and 1933; Sprehn, 1932; Theobald, 1896.

Description: Body length 9 mm., width 4-5 mm. Oral sucker 0.76-0.83 mm. or more in diameter, placed some distance posterior to the intestinal fork. Cirrus sac reaching to intestinal fork. Vitellaria begin at level of ventral sucker and extend posterior to testes, divided into follicular groups. Eggs: 0.027-0.029 mm. long by 0.011-0.015 mm. wide.

Hosts: oviduct: *Gallus domesticus, Anas boshas domesticus,* and from *Numenius arquatus.*

Geographical distribution: Northern Europe.

P. japonicus Braun, 1901a
(Plate III, Fig. 3)

Alessandrini, 1929; Braun, 1901a, 1902; Khaw, 1930; Lühe, 1909; Neumann, 1909; Shen, 1931; Sprehn, 1932.

Descriptions: Body 5 mm. long. Suckers nearly equal in size, 0.7-0.8 mm. in diameter. Intestinal fork much anterior to ventral sucker. Vitellaria begin in region of ovary, and extend much posterior to testes. Cirrus pouch very long and sinuous. Eggs: 0.024 mm. long by 0.012 mm. wide. From eggs of *Gallus domesticus* in Japan and China.

P. anatinus Markow, 1902
(Plate III, Figs. 1 and 2)
Lühe, 1909; Skrjabin, 1923; Sphehn, 1932

Description: Body 2.4-2.8 mm. long by 1.1-2 mm. wide. Ventral sucker two and one-half times size of oral sucker. Cirrus sac long and sinuous, reaching past intestinal fork. Vitellaria considerably restricted, beginning posterior to ventral sucker and reaching posterior end of testes (farther in figure). Ovary 3-4 lobed, behind ventral sucker. From bursa Fabricii of domestic duck (*Anas boshas domesticus*), in Russia.

P. putschkowskii Skrjabin, 1913
(Plate III, Fig. 4)
Baylis, 1929; Ono, 1930

Description: Body 7.3 mm. long by 4.85 mm. wide. Oral sucker 0.76-0.8 mm. long by 0.68 mm. wide. Ventral sucker 1.1-1.24 mm. in diameter. Testes 1.07-1.36 mm. long. Cirrus pouch sac 2.12 mm. long, reaching ventral sucker, and not much coiled. Vitellaria arranged in definite follicular groups, beginning at level of ventral sucker and extending posterior to testes. Eggs: 0.024 mm. long by 0.0145 mm. wide. From bursa Fabricii of *Platalea leucorodia* and *Gallus domesticus.* Aulie-ata, Syr Daria, Russian Turkestan; wide distribution through Russian Turkestan and Manchuria.

P. dogiele Skrjabin, 1914
(Plate IV, Fig. 4)
Sprehn, 1932

Description: Body length 4.75 mm., width 3.65 mm. Oral sucker 0.289 mm. by 0.314 mm. wide. Ventral sucker 0.85 mm. long by 1 mm. wide. Testes in middle third of body. Cirrus sac 0.883 mm. long, reaching only to intestinal fork. Ovary overlapping ventral sucker. Vitellaria begin anterior to ventral sucker and extend past testes, follicles very small and do not form separate clusters. Vitelline fields average 2.55 mm. long. Uterus with pre-acetabular loops. From bursa Fabricii of common swallow, *Hirundo rustica,* in British East Africa.

P. vitellatus Nicoll, 1915
(Plate IV, Fig. 2)
Baylis, 1929

Description: Body length 5 mm., width 2.6 mm. Oral sucker 0.53 by 0.33 mm. Ventral sucker 0.66 by 0.71 mm. Cirrus sac sinuous, extending slightly past intestinal fork. Testes large, 0.73 by 0.53 mm. in diameter, located just behind ovary in anterior half of body. Ovary dorsal to ventral sucker. Uterus considerably overlapping intestinal ceca. Eggs: average 0.028 by 0.015 mm. From bursa Fabricii of the drongo. *Dicrura bracteata* in Indo-China.

P. brauni Skrjabin, 1919
(Plate IV, Fig. 1)
Baylis, 1929; Skrjabin, 1923

Description: Body length 6.8 mm., width 5.46 mm. Oral sucker 0.57 mm. long by 0.49 mm. wide. Ventral sucker 0.89 mm. in diameter, located immediately after intestinal fork. Base of cirrus sac to anterior end of body, 1.43 mm. Testes 1.06-0.94 mm. long by 0.94-0.86 mm. wide. Eggs: 0.023 mm. long by 0.013 mm. wide. Vitellaria divided into 7-8 distinct groups, fields begin just anterior to the ventral sucker and extend somewhat posterior to the testes. From bursa Fabricii of the domestic hen in the Don Region of Russia.

P. rudolphii Skrjabin, 1919
(Plate II, Fig. 3)

Description: Body length 5.78 mm., width 1.79-2 mm. Oral sucker 0.385 mm. long by 0.36-0.338 mm. wide. Ventral sucker 0.77-0.71 mm. long by 0.8-0.7 mm. wide. Testes 0.37-0.5 mm. in diameter, located posterior to the ventral sucker to somewhat behind the testes; follicles arranged in 6-8 clusters on each side of the body. Cirrus sac sinuous. Uterine coils intercecal. From bursa Fabricii of domestic duck (*Anas boshas domesticus*) in the Don Region of Russia.

P. skrjabini Zakharow, 1920
(Plate IV, Fig. 5)
Baylis, 1929; Skrjabin, 1923; Sprehn, 1932

Description: Body length 4.54 mm., width 2.85 mm. Oral sucker 0.338 mm. in diameter. Ventral sucker 0.847 mm. long by 0.86 mm. wide. Testes 0.246-0.308 mm. in diameter. Base of cirrus sac 0.97 mm. from anterior end of body. Vitelline follicles minute, arranged in clusters, beginning at level of ventral sucker and ending behind testes. Uterine coils intercecal. Bursa Fabricii of domestic duck and "quack duck" in the Don Region of Russia.

P. furcifer Railliet, 1924
(not illustrated)
Baylis, 1929; Sprehn, 1932

Description: Body length 8.5 mm., width 5.7 mm. Suckers subequal, each about 1 mm. in diameter. Cirrus sac extending past intestinal fork and reaching almost to acetabulum. Ovary post-acetabular. Vitellaria begin at the anterior border of the ventral sucker and reach just posterior to the testes. From bursa Fabricii of domestic hen in Indo-China.

P. horiuchii Morishita and Tsuchimochi, 1925
(Plate II, Fig. 2)
Morishita, 1929

Description: Body 5.6-8.9 mm. long by 2.39-4.86 mm. wide. Oral sucker 0.26-0.4 mm. by 0.4 mm. in diameter. Ventral sucker two and one-half times size of oral sucker. Vitellaria begin back of acetabulum and end posterior to testes. Eggs: 0.026 mm. long by 0.013 mm. wide, with a knob at the posterior pole. Found in one-fourth of the domestic ducks and in one-half of the domestic geese of Formosa.

P. fuelleborni Skrjabin and Massino, 1925
(Plate III, Fig. 5)

Description: Body length 2.28 mm., width 1.17 mm. Oral sucker, length 0.2 mm., width 0.296-0.257 mm. Ventral sucker 0.855-0.778 mm. long by 0.534-0.672 mm. wide, located in the middle third of the body. Cirrus sac 1.04 mm. long. Ovary behind ventral sucker. Vitellaria begin at level of ventral sucker and extend posterior to testes. Eggs: 0.033-0.028 mm. long by 0.019-0.014 mm. wide. From the bursa Fabricii of the common European jay, *Garrulus glandarius,* in the region of Moscow, Russia.

P. karausiaki Layman, 1926
(Plate IV, Fig. 3)

Description: Body length 2.28 mm., width 1.71 mm. Oral sucker, length, 0.2 mm., width 0.17 mm. Ventral sucker, length 0.456 mm., width 0.399 mm. Cirrus sac 0.57 mm. long. Vitellaria begin at the level of the ventral sucker and end just posterior to the testes. Eggs: 0.024-0.028 mm. long by 0.0145 mm. wide. From the bursa Fabricii of a pheasant, *Phasianus mongolicus turkestanicus,* in the village of Kara-Uziak, Turkestan.

If spines are constantly absent from *P. orientalis* Yamaguti, 1933, it may be a good species, but otherwise it is probably synonymous with *P. anatinus* Markow. It is also probable that *P. querquedulae* Yamaguti, 1933, is referable to *P. putschkowskii* Skřjabin.

There is such a close resemblance between *P. anatinus, P. skrjabini,* and *P. karausiaki* that all of these may possibly be referable to *P. anatinus.* Likewise, *P. horiuchii* may be synonymous with *P. putschkowskii.* Seifried, 1923, described a new species which he termed *P. longus morbificans* (*P. longus morbificans,* Baylis, 1929; *P. longus,* Skrjabin, 1925; *P. longus-morbificans,* Shen, 1931), ignoring the binomial system required by the international rules of zoological nomenclature. His specimens differ from *P. pellucidus* in that the ventral sucker is one-half larger than the oral sucker, and differ from *P. macrorchis* in that the cirrus sac in his form reaches the ventral sucker.

Specific Characters in the Genus *Prosthogonimus*

Because of the individual variation, great caution must be exercised in identifying specimens of the genus *Prosthogonimus.* The application of too much pressure at the time of mounting will cause the distortion of the testes and may shift their position. Characteristics of young examples may be misleading, and for this reason only fully developed ones should be used for identification purposes.

Variation of characters upon which the specific characters are based demands description made from a large series of specimens. Judging from measurements of numerous individuals of *P. macrorchis,* and from the work of investigators of other species, the following appear to be reliable specific characters: Considerable differences in the length of the cirrus sac; length of the vitelline fields; ratio between the size of the oral and ventral suckers; relation in position between ovary and testes, and between ovary and ventral sucker; position of vitelline fields in relation to the ventral sucker, ovary, and testes; relation between intestinal fork and ventral sucker; presence or absence of heavy uterine coils anterior to ventral sucker; extent of uterine coiling in posterior part of body; and relation of intestinal ceca and posterior uterine slings. Size of the testes and ovary is subject to too much variation to be of much use in this connection. The length of spines is of possible use, but is unrecorded for many species.

Experiments on the rearing of *P. macrorchis* in various hosts suggests the possibility that further life history investigations and measurements of large series of specimens will lead to a substantial reduction in the number of described species.

GEOGRAPHICAL DISTRIBUTION

While species of the genus *Prosthogonimus* are known to occur on the five continents, investigation of the distribution of the group has been restricted to very small areas. Rapidly accumulating data indicate that the species will be found to have a far greater range than is now recorded. Occurrence of many of the species in migratory birds and domestic fowls and lack of great host specificity account in a large measure for widespread distribution.

In North America, *P. macrorchis* has thus far been recorded only from the Great Lakes region. Dr. W. A. Riley (unpublished data) first noticed the typical cysts in dragonfly adults and naiads in Minnesota in 1924, and has records of the common occurrence of the fluke in domestic hens in Western Ontario, Canada, in 1928. Linton, 1887, observed this species from Wisconsin, and Kotlan and Chandler, 1925 and 1927, reported it from Muskegon, Michigan. Lakela, 1931, showed it to be present at Glenwood Lake, Minneapolis. The writer has identified as *P. macrorchis* flukes taken from hen's eggs at Hines, Beltrami County, and at Grand Rapids, Itasca County, Minnesota.

The writer examined dragonflies from Crystal Lake, Glenwood Lake, Medicine Lake, and Lake Minnetonka in Hennepin County; Lake Johanna, McCarron's Lake, Lake Owasso, Round Lake, Sucker Lake, Lake Vadnais, and Lake Valentine in Ramsey County; Lake Itasca in Clearwater County; and Detroit Lakes in Becker County. Of these, Crystal, Glenwood, Minnetonka, Valentine, Itasca, and Detroit Lakes had dragonflies infested with *Prosthogonimus* cysts.

Absence of the parasite from some of the lakes surveyed may be partially accounted for by the infrequency of the visits of suitable definitive hosts to these places. During the period of observation no domestic birds were seen along the shore of any lake visited; indeed the tendency of the farmers of the Twin Cities region is to keep poultry away from the lake-shore by fencing, without any consideration of possible parasitism.

The heavy incidence of this trematode in the dragonflies of Glenwood Lake may be accounted for by the presence of about 50 tame mallard ducks and large numbers of suitable insect and snail hosts.

As to the occurrence of other species of the genus in Minnesota, we know little as yet. Szidat, 1933, pointed out that there are comparatively few ducks killed by hunters during the spring, when the oviducts are functional and therefore favorable for *Prosthogonimus* invasion. For this reason, few carcasses reach the parasitologist at the most favorable time for finding the species of this genus. Nevertheless, Dr. Riley has found numbers of *Prosthogonimus rudolphii* (Plate IX, Fig. 5) in tame mallard ducks in early June, from Little Pelican Lake, Becker County, Minnesota. Considering the large numbers of species found elsewhere, it is to be expected that other North American forms will eventually be found.

GROSS AND HISTOLOGICAL MORPHOLOGY

Adult

In its living condition, the marita of *Prosthogonimus macrorchis* exhibits blackish uterine coils, in contrast to the slightly pinkish cream color of the pyriform body, which lies limply on the parasitized tissue. The cuticula of a sectioned individual is 15-20 μ thick (Plate V, Fig. 1), and lies on a thin layer of longitudinal muscle which is bounded on either side with more or less irregularly arranged circular muscle fibers. The spines, imbedded in the substance of the cuticula, are braced against the longitudinal muscle layer and reach the surface in cuticular grooves (Fig. 1, cg.). The number of spines is greatest at the anterior end of the body but a few even occur at the posterior end. These latter are blunt (Fig. 2), expanded at the distal end, and show evidence of structural design. Such spines measure 18 μ long and up to 8.7 μ wide, while those located anteriorly are sharp-pointed, slant caudad, and measure about 26 μ long by 3.5 μ wide at the base.

The length of cuticular spines is given by Skrjabin, 1913, as 20.3-33.2 μ in *P. putschkowskii,* 15 μ in *P. ovatus,* and 15.5 μ in *P. cuneatus.* In *P. macrorchis* the arrangement of spines on the surface of the body (Plate V, Fig. 3) does not appear to follow a very definite pattern.

Aside from the muscles of the body wall, of the suckers, pharynx, and of a few of the other organs, there is little evidence of further musculature. There are, however, some transverse fibers, and also a fair development of oblique fibers, the latter being observed as attached to the body wall from where they run entad and caudad. Suckers and pharynx are composed almost entirely of elongate muscle cells with fibrillar cytoplasm and nuclei containing little chromatin. Sluggish mobility and the collapsed appearance of the living fluke attest to the poor development of the muscular system. The bulk of the body is composed of greatly vacuolated, somewhat irregularly arranged parenchymal cells which have relatively small nuclei.

Oral aperture, pharynx, short oesophagus, and long intestinal ceca comprise the digestive system. The intestinal bifurcation is located about midway between the pharynx and the ventral sucker, where it divides into two, relatively wide ceca which nearly reach the posterior end of the body.

The columnar epithelial cells which line the ceca average 30 μ in height (Plate V, Fig. 7). The distal ends of these cells are irregular and vacuolated. The cytoplasm is finely reticular and frequently shows granular and fibrillar phases, especially at the basal end, which is bounded by a basement membrane. There is little evidence of muscle fibers in connection with this part of the digestive system.

Considering first the male parts of the reproductive system, the testes are large, spherical to ovate, entire, located opposite each other in the third fourth of the body length, and are definitely posterior to the ovary. In section, the peripheral layer of the testis is composed of great numbers of proliferating cells and forms the densest region; the interior consists of numerous groups of spermatozoa in the process of maturation. Judging from the great numbers of sperm cells crowding the vas deferens, there must be a tremendous output of these elements. The sperm cells themselves, unlike those seen and illustrated for many kinds of trematodes, have considerably enlarged and rounded heads. Arising from the anterior periphery of the testes, the vasa efferentia pass forward, somewhat below the dorsal body surface, and unite in the vicinity of the ventral sucker, frequently at the posterior margin, to form the vas deferens which leads directly to the posterior margin of the cirrus sac where it enters the wall of that body and empties into the much-coiled seminal vesicle (Plate VIII, Fig. 6). The latter lies in the posterior half of the cirrus sac, narrowing anteriorly into a duct which leads to the poorly developed cirrus. A valve lies between the efferent duct of the seminal vesicle and the cirrus. The male genital pore, through which the cirrus may protrude, lies alongside the female genital pore on the left side of the oral sucker. Parenchymal cells of the cirrus sac (Plate V, Fig. 9) are heavy-walled and contain nuclei which have finely divided chromatin and centrally placed nucleoli. The wall of this pouch is provided with a rather heavy coat of longitudinal muscles.

The ovary lies posterior to the ventral sucker and slightly to the right of the body axis. It is of irregular shape and size and consists of 3 to 15 closely clustered lobes, similar in appearance to those described for the other members of the genus. As shown in the diagram (Plate V, Fig. 6), the oviduct joins the posterior part of the ovary with the oötype, meanwhile receiving the duct from the seminal receptacle and the common yolk duct. Eggs leaving the ovary pass down the oviduct to the oötype where the shell is shaped around the egg cell and its three to five yolk cells, which are added from the yolk reservoir. In the region of the oötype there is seen the dense cytoplasm of converging Mehlis' gland cells (Plate V, Fig. 10). Laurer's canal leaves the dorsal surface of the body somewhat to one side of the seminal receptacle, extends over a tortuous course which leads caudad for some distance and then returns cephalad to empty into the posterior, lateral, or dorsal side of the seminal receptacle. In this case, Laurer's canal is probably functional, acting as a vagina, for it reaches the surface of the body, spermatozoa are seen in its lumen, and the walls are highly developed. The walls are about 18-20 μ thick, lined with columnar epithelium, and furnished with a well-developed musculature consisting of an inner, longitudinal layer and an outer, circular layer.

Continuous with the oötype is an enormously developed, egg-filled uterus, consisting of descending limb, ascending limb, and metraterm or muscular portion leading anteriorly to the female genital pore. The walls of the descending and ascending portion consist of elongate, flattened cells capable of considerable distension (Plate V, Figs. 4 and 5).

The vitellaria consist of eight or nine lateral, follicular clusters, connected by plainly differentiated collecting tubules, which, in turn, lead to the prominent yolk ducts. Each of the follicular groups consists of several arms radiating from their union with the collecting duct.

The golden-brown eggs are rather thick-shelled and operculate (Plate I, Figs. 2 and 3). Their shape is subject to considerable variation, with the normal types resembling, to a moderate extent, the eggs of *Clonorchis sinensis*. At the caudal pole there is a twisted spine of variable shape and length. In one instance this spine was as long as the rest of the egg. The eggs average 28 μ long by 16 μ wide and contain embryos at the time they are laid.

Only the more prominent parts of the excretory system can be followed in the adult. The large, Y-shaped excretory vesicle empties posteriorly on the ventral surface of the body. Bifurcation of the bladder occurs in the mid-body region and considerably posterior to the ventral sucker. A more detailed account of the excretory system is given with the description of the metacercaria.

Altho a detailed study of the nervous system was not attempted, many of its features could be seen. There are important nerve centers at the anterior and posterior borders of the pharynx, and surrounding the ventral sucker. From these centers numerous nerve fibers radiate to all parts of the body. Many large and striking bipolar nerve cells occur throughout the body, along the pathways of the connectives and between the muscle cells of the suckers and pharynx. As seen in section, a typical nerve cell, measuring 54 μ long by 22 μ wide, exhibits a coarsely fibrillar cytoplasm and a light-staining nucleus, 12.6 μ long by 10.8 μ wide, with a large, spherical, deep-staining nucleolus.

Sporocyst

Cigar-shaped, 0.1 mm. long by 0.4 mm. wide, the sporocyst consists of a thin-walled sac containing germ balls and developing cercaria, the number of which may vary considerably. In the younger sporocysts (Plate VI, Fig. 3) there are germ balls only, while in later stages (Fig. 4) there are developing cercariae, which early give evidence of round tailbuds. A later, intermediate stage (Plate VI, Fig. 4, dc) develops a refractile cuticula and an oral sucker, but as yet reveals no visible indication of the ventral sucker. Separation of the sporocyst from the "liver" tissue of the snail, in which it lies imbedded, is difficult, and many times the sac bursts during the operation, releasing numbers of mature, actively swimming cercaria. No redia form is present in the development of this trematode.

Cercaria

The relatively small, elongate cercaria (Plate VI, Fig. 2), because of its simple tail and the presence of a stylet in the oral sucker, is a typical xiphidiocercaria, according to the classification of Lühe, 1909. In average length the body measures 152 μ, and in width 64 μ, altho the body is frequently stretched to a much greater length, producing a lessened width. The tail with its characteristic alternating creases measures 48 μ long by 18 μ wide. Minute striations appear in the body cuticula. The oral sucker is well developed. It is 40 μ in diameter and contains a stylet 15 μ long by 4 μ wide. Altho a small pharynx is visible behind the oral sucker, no more of the digestive system can be seen. Placed in the posterior half of the body, the ventral sucker, which is rather poorly developed, is 24 μ in diameter. On either side of the ventral sucker are four prominent penetration gland cells (pg) with ducts leading to the anterior edge of the oral sucker. Near the outer margin of the body, in the posterior half and lying laterally on either side, there are a number of dark areas consisting of concentrations of granules which exhibit marked Brownian movement. The sole structure which indicates the taxonomic relationship of the cercaria is the shape of the excretory bladder, a Y-shaped structure, which undergoes periodic contractions. A few of the fine collecting tubules of the excretory system could be seen but their relationships were not clear. It is to be noted that, as in the other xiphidiocercaria (Cort, 1915), the internal structures are very difficult to study because of the opaque nature of the parenchyma. Even so, most of the internal organization is best studied while the cercaria is yet alive.

Metacercaria

There was great difficulty in identifying internal structures of the metacercaria until after full size was attained. Between the youngest observed metacercaria, 16 hours after penetration, and the largest stage, only the prominent Y-shaped excretory bladder, the suckers, and the pharynx could be found. Experimental growth-stages are described in a later section.

For studying the full-grown metacercaria, the heavy cyst wall was digested off, the worms were slightly compressed between slide and cover, and were killed and mounted by the same methods used for the adult flukes. For the study of the excretory system, only living examples were used.

The excretory bladder is now filled with highly refractive granules, and the finer details of the system are to be seen (Plate VIII, Fig. 2). The flames cells are arranged in pairs and their capillaries arise directly from the principal collecting tubules. The first pair lies at either side of the oral sucker; one of the second pair lies near the collecting tubule and is placed near the anterior edge of the ventral sucker; the cells of the third pair are similarly separated with one of them lying along the posterior margin of the ventral sucker; and the members of the following three pairs are situated close together. The fifth set of cells lies in the vicinity of the termination of the intestinal ceca. Following the type of formula used by Faust, 1929, to designate the arrangement of the flame-cells, the flame-cell pattern of the metacercaria of *P. macrorchis* may be expressed as follows:

$$2\ [\ (2+2+2)+(2+2+2)\ ]$$

In this case, the first number "2" represents the bilateral condition, the parentheses indicate the groups in the anterior and posterior halves of the body, and the enclosed figures point out that the flame cells are arranged in groups of two each.

Another feature of the living, infective metacercaria is the presence of numerous gland cells and their ducts extending across the body in front of the ventral sucker. Their secretion may perhaps aid the trematode in its escape from the thick cyst.

In stained preparations (Plate VIII, Fig. 1) the body measures 0.6 mm. long by 0.27 mm. wide and the oral sucker is 0.08 mm. in diameter as compared to the slightly larger ventral sucker which measures 0.1 mm. in diameter. Following the muscular pharynx is the relatively short oesophagus, which forks into the long ceca at a point situated from one-half to two-thirds of the distance from the oral to the ventral sucker. The ceca reach a point just past the bladder bifurcation, over three-fourths of the distance to the caudal end of the body.

Of the reproductive system, the primordia of the testes, ovary, uterus, and cirrus sac are plainly evident (te; ov; ut; cp).

BIOLOGY

Adult

Host specificity and natural reservoirs.—Skrjabin and Baskakow, 1925, after the examination (1918-1922) of 3,792 birds comprising 244 species, were able to draw a number of conclusions of great interest concerning host specificity and natural reservoirs of avian helminths.

They found 53.44 per cent of the birds had parasitic worms and that of the total number examined, the water birds were the most heavily parasitized. Among the young birds, *Prosthogonimus* was found in 15.7 per cent of those in the Don region (Russia), 5.6 per cent in the Moscow region, and 10.8 per cent in Turkestan. The highest numbers of *Prosthogonimus* found in one host (*Pica caudata*) were 42 and 53, in the Don region and in Turkestan, respectively. Of the birds infested with worms, *Prosthogonimus* represented 26.7 per cent of the total in the Don region. Excluding young birds, *Prosthogonimus* invasion represented 44 per cent of the total in the Moscow region and 56.3 per cent in Turkestan. One host, *Merops apiaster,* carried *Prosthogonimus* but no other parasitic worms. Of the total parasitized by *Prosthogonimus,* 72.4 per cent were land birds and only 27.6 per cent were water birds. Species of *Prosthogonimus* more commonly infested migratory species than permanent residents. Species were not found to prefer any certain order of birds, since of the 14 orders of birds represented in their collections, only the Columbae and Pici were found to be uninfested by them. Of the total cases of *Prosthogonimus* infestation, 186 were confined to the bursa Fabricii and only five elsewhere (large intestine three times, small intestine once, and cloaca once).

In order to obtain data concerning the host specificity of *P. macrorchis,* red-wing black birds, crows, sparrows, a wild mallard duck, and a number of domestic ducks were fed cysts of this trematode taken from Glenwood Lake, Minneapolis.

Through the courtesy of Mr. Ralph T. King, an adult mallard duck, *Anas platyrhynchos,* taken from an artificial breeding ground for wild ducks, was obtained for experimental purposes. On May 24 it was fed 50 infected *Tetragoneuria* naiads. These were previously placed in a shallow tank in order to note the duck's ability to see them under water. After being placed in the tank, the mallard, with very little hesitation, reached under the water for the insects and devoured every one in a surprisingly short period of time. Undoubtedly immature naiads of dragonflies, found in clear water near the shore, are often caught by ducks and aid in keeping *Prosthogonimus* infestation at a higher level. When this infested duck was opened, three weeks later, no flukes were found, probably because the bursa Fabricii had atrophied.

Two young crows, *Corvus brachyrhynchos,* about three-fourths grown, taken from a nest far from any lake, and which showed no parasitic eggs in the feces, were fed five infested *Tetragoneuria* naiads each on May 25, and 10 more each on May 30. The bursa Fabricii of the first crow, killed June 10, yielded seven mature *Prosthogonimus macrorchis* (Plate IX) and one much smaller specimen. The first group of parasites was 17 days old, and the second 12 days old, the worms presumably developing from the first and second feedings, respectively. The other crow, killed June 19, had no *Prosthogonimus* infestation.

A nestling English sparrow, *Passer domesticus,* was fed 10 *Leucorrhinia* June 7; 4, June 8; 4, June 9; and 2 more, June 10. It was killed late on June 10 and 72 immature *Prosthogonimus,* varying slightly in size, were found in the bursa Fabricii and in the lower intestine.

A second English sparrow nestling was fed 10 cysts July 19 and 10 more on July 23. August 2, 14 days later, 8 mature *Prosthogonimus macrorchis* and 2 immature specimens were recovered from the bursa Fabricii of this bird, which had meanwhile developed sufficient plumage to enable it to fly with ease. (See Plate IX).

Both of the sparrows, as well as the other birds used in experiments, were taken from nests far from any lakes and were therefore believed to be free from previous infestation. Even with frequent feedings of earthworms, bits of beef and mash, there was a high mortality among experimental nestlings. One English sparrow taken from a nest on the Zoology Building was confined in a cage just inside an open window and was cared for by its mother.

Three red-wing blackbird nestlings (*Agelaius phoeniceius*) were fed 20 *Prosthogonimus* cysts each on July 18 and were examined July 22, after death, but no parasites were found.

Twelve domestic ducks were infested, as shown in Table 9, and the results indicate that they are favorable hosts for *Prosthogonimus macrorchis.* Domestic chickens fed (Table 8) indicate that they are favorable hosts, but that they lose their infestation early.

From observation and from personal interviews with the superintendent of Glenwood City Park and the superintendent of the Municipal Park-Board Nursery, who live on the lakeside, it can be said that no chickens have access to Glenwood Lake or have had any opportunity to run there for a number of years. It is therefore assumed that the cysts of *Prosthogonimus* taken from the dragonflies of this lake, which is situated within the city of Minneapolis, are those of *Prosthogonimus macrorchis* and that the heavy infestation is maintained by a flock of 50 mallard ducks kept there by the city Park Board.

On June 18, 1932, some time was spent observing the efforts of the Glenwood mallards to capture the numerous dragonflies clinging to reed stems or cruising about in the vicinity of the ducks. Altho none were captured by them during the period of observation, it is probable that in the course of time a considerable number was eaten. The ability of the captive mallard to catch naiads under water has already been described. As to the sparrows, Dr. Riley (unpublished data), during the course of his investigations at Detroit Lakes, Becker County, Minnesota, took a large number of immature *Prosthogonimus* from the bursa Fabricii of English sparrow nestlings which were being fed dragonflies by the mother bird. Crows would undoubtedly eat dragonflies if they could get them, and the fact that various European crows harbor species of the genus is evidence that they do catch them. According to a United States Biological Survey chart (Roberts, 1932), about a third of the food of nestling red-wing blackbirds consists of dragonflies, so that they would have an excellent chance to become infested with *Prosthogonimus* if they are capable of harboring this parasite.

If longevity and pathological effects of a trematode indicate the extent of compatibility of a host for a parasite, one may believe that ducks are the normal definitive hosts for *Prosthogonimus macrorchis* in nature, and that domestic chickens are less favorable hosts. As evidence of this, it has also been found that this form is harmful to chickens and is ordinarily lost in a period of from three to five weeks.

Feeding experiments previously described indicate that crows and sparrows may act as reservoirs in nature. A survey of the hosts of European species of the genus suggests other possible hosts for our species in North America. Of particular interest in this connection is the survey of Skrjabin and Baskakow, 1925, previously reviewed, in which the authors found the following list of birds infested with *Prosthogonimus* (species not given):

Actitis hypoleucos	sandpiper
Anas boshas	common duck
Hydracorax niger	
Fulica atra	coot
Larus canus	gull
Porzana maruetta	rail
Rallus aquatis	European water rail
Scolopax gallinago	shore bird
Himantopus cand	stilt

Larus cochin	gull
Corvus frugilegus	rook
Cotyle riparia	bank swallow
Delicon urbica	
Hirundo rustica	European swallow
Emberiza hortulana	Ortolan bunting
Gallus gallus domesticus	domestic hen
Falco tinnunculus	kestrel
Falco vespertinus	
Fringilla montifring	sparrow
Lanius collurio	shrike
Lanius minor	shrike
Meleagris gallopavo	turkey
Merops apiaster	European bee-eater
Motacilla alba	white wag-tail
Motacilla flava	yellow wag-tail
Passer domesticus	English sparrow
Pica caudata	magpie
Saxicola isabellina	wheat-eater
Surnus vulgaris	English starling
Upupa epops	hoopoe
Cherchneis tinnunculus	
Merops persicus	bee-eater
Corvus cornix	crow
Garrulus glandarius	European jay

These 34 species of birds represent the seven following orders (Skrjabin and Baskakow): Raptores, Passeres, Macroschires, Coccygomorphae, Gallinacei, Grallatores, Lamellizostres, Ciconiae, Longipenes, Pygopodes, and Steganopodes. Other hosts of the group include geese, doves, many species of ducks, gallinules, pheasants, egrets, cranes, teals, swans, drongos, and a few more.

Variation and host influence.—The examination of specimens of *P. macrorchis* from a variety of experimentally-infested birds indicates that the hosts and organs (oviduct or bursa Fabricii) may have a considerable effect on such parasites.

Occasionally the ventral sucker is found to be nearly twice the size of the oral sucker, altho the variation is usually slight. Length of the oesophagus depends on the amount of extension of the anterior part of the body at the time of death, and the location of the intestinal fork may vary somewhat but is usually from one-third to one-half the distance from oral to ventral sucker. In the great majority of cases the follicular grouping of the yolk follicles of oviduct-produced flukes has the arrangement shown in the figure of the type (Plate I, Fig. 1). Rarely there is a compact arrangement whereby the grouping is hardly discernible. The number of lobes in the ovary may vary from three to twenty or more, and the ovary may be longer than broad or *vice versa,* usually the latter. Egg masses occasionally form ahead of the ventral sucker, enlarging the metraterm. Size of the testes is subject to considerable variation, but there is a definite size range depending on the host and location within the host. Sometimes the vitelline field of one side is greatly shortened and the testis of the same side may be very much smaller than its mate. Similarly, one frequently finds appreciable difference in the lengths of the intestinal ceca in the same specimen. It also may be mentioned that some specimens are truncate and therefore abnormally shortened.

Table 2

Measurements of *P. macrorchis* from bursa Fabricii of Chick

	No. 1	No. 2	No. 3
Body length (mm.)	4.8	4.5	4.0
Body width	3.6	3.3	3.0
Oral sucker, length	0.306	0.380	0.342
Oral sucker, width	0.396	0.380	0.360
Ventral sucker, length	0.666	0.576	0.576
Ventral sucker, width	0.648	0.594	0.612
Pharynx, length	0.144	0.198	0.162
Cirrus sac, length	0.612	0.720	0.648
Testes, length	0.972–0.936	0.630–0.576	0.252–0.252
Testes, width	0.684–0.630	0.468–0.522	0.216–0.180
Ovary, length	0.882	0.576	0.252
Ovary, width	0.580	0.540	0.342

Table 3

Measurements of *P. macrorchis* from the Domestic Duck

	No. 1	No. 2	No. 3	No. 4
Body length (mm.)	5.2	4.9	4.0	6.3
Body width	4.0	3.0	4.0	2.0
Oral sucker, length	0.342	0.324	0.306	0.360
Oral sucker, width	0.342	0.342	0.360	0.486
Ventral sucker, length	0.612	0.576	0.540	0.702
Ventral sucker, width	0.648	0.558	0.612	0.774
Pharynx, length	0.162	0.144	0.162	0.216
Pharynx, width	0.126	0.162	0.126	0.306
Cirrus sac, length	0.774	0.702	0.630	0.990
Testes, length	0.432–0.540	0.378–0.360	0.504–0.316	0.1008–0.1206
Testes, width	0.648–0.462	0.450–0.414	0.360–0.432	0.567–0.630
Ovary, length	0.702	0.432	0.324	0.666
Ovary, width	0.558	0.486	0.792	0.540

Nos. 1, 2, and 3, from the bursa Fabricii
No. 4, from the oviduct

Table 4

Measurements of *P. macrorchis* from the bursa Fabricii of the Crow (*C. brachynchos*)

	No. 1	No. 2	No. 3
Body length (mm.)	4.0	4.0	3.9
Body width	2.3	1.9	2.0
Oral Sucker, length	0.396	0.306	0.324
Oral sucker, width	0.396	0.326	0.360
Ventral sucker, length	0.612	0.612	0.594
Ventral sucker, width	0.612	0.630	0.594
Pharynx, length	1.162	0.180	0.126
Pharynx, width	0.190	0.198	0.162
Cirrus sac, length	0.558	0.720	0.468
Testes, length	0.522–0.612	0.540–0.720	0.540–0.450
Testes, width	0.396–0.378	0.360–0.342	0.216–0.288
Ovary, length	0.270	0.288	0.234
Ovary, width	0.588	0.588	0.378

Table 5

Measurements of *P. macrorchis* from bursa Fabricii of the English Sparrow (*P. domesticus*)

	No. 1	No. 2	No. 3
Body length (mm.)	2.8	2.5	2.6
Body width	1.7	1.4	2.0
Oral sucker, length	0.234	0.198	0.240
Oral sucker, width	0.234	0.234	0.270
Ventral sucker, length	0.396	0.396	0.414
Ventral sucker, width	0.486	0.432	0.414
Pharynx, length	0.126	0.108	0.126
Pharynx, width	0.090	0.126	0.126
Cirrus sac, length	0.450	0.414	0.540
Testes, length	0.342–0.306	0.371–0.288	0.360–0.360
Testes, width	0.342–0.270	0.288–0.240	0.306–0.342
Ovary, length	0.288	0.252	0.234
Ovary, width	0.486	0.234	0.486

Table 6

Measurements of *P. macrorchis* from Different Hosts, from an Average of Three Specimens Each

	English sparrow	Crow	b. Fab. duck	b. Fab. chick	Hen oviduct
Body length (mm.)	2.6	3.97	4.7	4.43	7.36
Body width	1.7	2.07	3.66	3.3	5.43
Oral sucker, length	0.226	0.342	0.324	0.342	0.486
Oral sucker, width	0.269	0.360	0.448	0.378	0.486
Ventral sucker, length	0.402	0.606	0.576	0.606	0.691
Ventral sucker, width	0.444	0.612	0.606	0.618	0.822
Pharynx, length	0.120	0.156	0.156	0.168	0.222
Pharynx, width	0.116	0.183	0.138	0.180	0.210
Cirrus sac, length	0.468	0.582	0.535	0.660	0.900
Testes, length	0.387	0.564	0.421	0.601	1.774
Testes, width	0.696	0.660	0.461	0.450	1.341
Ovary, length	0.258	0.266	0.486	0.572	0.882
Ovary, width	0.402	0.508	0.612	0.487	1.320

A crow, *Corvus brachyrhynchos,* experimentally infested in our laboratory, produced six fully-matured specimens of *Prosthogonimus macrorchis,* extending posterior to the testes, and the ratio between the average diameter of the oral and ventral sucker was 1:1.8. Except for slightly greater differences in the size between the suckers and the placement of the ovary nearer to the ventral sucker, the specific characters hold for specimens reared in this host (Table 4).

Another bird, the English sparrow, *Passer domesticus,* also produced mature *P. macrorchis* (Plate IX) in the bursa Fabricii. Altho the specimens were smaller in size, the specific characters were also found to fit this variation. Of the three specimens measured, the ratio of the oral to the ventral sucker was 1:1.7. There was some tendency for the vitellaria to extend posterior to the testes, altho this was not marked. (Table 5.)

In the example reared in the oviduct of the domestic duck, *Anas boshas domesticus* (= *Anser platyrhynchos domesticus*), the ratio between oral and ventral sucker is 1:1.7, and the vitelline fields do not extend past the testes (Plate IX). On the other hand, specimens from the bursa Fabricii present a very different appearance. Yet the ratio between the suckers remains 1:1.7. Here the vitellaria do not extend posterior to the testes, but the latter organs are very small (Plate IX). In these flukes there is a marked increase in the width of the body, so that this dimension may nearly equal the length.

There is a striking similarity between those specimens from the bursa Fabricii of the duck and those reared by Lakela in the same organ in the chick infested while very young. In the latter host the sucker ratio is also 1:1.7, and the distribution of vitellaria is as it was in the former host.

It then appears that sucker-size ratio is the most constant of the specific characters when considering host-modified forms. Except in the form developed in the crow, the cirrus sac is uniformly straight and ends near the intestinal fork, save in a few of the largest of these flukes from the hen, in which instances it has been seen to extend some distance posterior of that point. In the specimens from the crow, the cirrus sac is frequently sinuous. The form of the uterus is very characteristic for examples from each type of host. In those from the crow it fills the posterior half of the body with dense coils, which now and then partly obscure the testes. Its coils are arranged in a striking pyramidal pattern in the examples from the bursa Fabricii of the duck and the chick. Those found in the oviduct of the hen and duck have the pattern shown in the type. In the smaller specimens, as those from the crow and the sparrow, the vitelline follicles are not arranged in such definite groups as in the type (Plate I, Fig. 1). The testes of *P.*

macrorchis reared in the bursa Fabricii of the various hosts are noticeably smaller, often strikingly so, compared to those from the oviducts of hens and ducks.

Judging from the cases at hand, variation of structure in our specimens is due more to the habitat within the host than to the host. In the one case there are the two diverse forms occuring in the oviduct and in the bursa Fabricii of one host (duck) and in the other instance there are the different forms from crow and chick (both in the bursa Fabricii). Taking the case of two rather distantly related hosts, the domestic hen and the domestic duck, it is found that those specimens from the oviducts of both resemble each other much more closely than they do those from the bursa of the two hosts. Invariably the testes are smaller, the width of the body is increased, and the vitellaria are more compact in the latter instance. No such marked differences occur in the oviduct forms.

Inspection of the peculiarities of other species, viewed in this light, suggests the possibility that *P. skrjabini, P. karausiaki,* and *P. anatinus* may be bursal modifications of some other species occurring in the oviduct.

The various modification groups obtained by the experiments were all produced by the one type of cyst from Glenwood Lake, where a flock of tame mallard ducks is the probable cause of high infestation. None of the other investigated lakes of the surrounding country yielded more than one-tenth of such infestation, nor had they such permanent flocks of hosts, and as all of the specimens reared in the birds were evidently of one species, it may be believed that the vast majority of specimens must represent one species. Conclusive proof, however, must be furnished by further rearing experiments.

Growth and longevity.—Numerous feeding experiments enable one to state that in the oviduct of the hen growth of this trematode is rapid, perhaps due to abundant secretion of the oviduct, and maturity may be reached in the remarkably brief period of one week. Maximum size of the worms is not reached for three or four weeks and their size tends to be larger when few are present. Flukes exist for a relatively short period in the hen oviduct, being lost in from three to six weeks.

In ducks, growth is slower, full size not being reached for about three weeks, and when this maximum (smaller than in those from hen) is attained it does not appear to increase, even after several months' time. One duck, C1481, killed four and one-half months after infestation, still harbored two characteristic *P. macrorchis* in the bursa Fabricii. Growth rate appears to be similar for individuals grown in chick and duck. Specimens reared in the crow reached maturity in 16 days, and those produced in the sparrow were mature, though small, at the end of 14 days.

Atrophy of the bursa Fabricii took place in the ducks when they were about seven months old, resulting in the loss of the structure which supports the flukes in the duckling. No bursa was found in any of the adult chickens and it is therefore evident that it atrophies by the time maturity is reached. As suggested by Skrjabin and Baskakow, 1925, there is a greater opportunity for young birds of many kinds to harbor *Prosthogonimus* because of the temporary presence of the bursa Fabricii and this was borne out by the results of their extensive dissections. In mature birds, then, the oviduct in many cases is the sole organ which can support the existence of this group of trematodes, and this, only for the short, functional season of this structure.[3] Domestication has modified the condition in the hen so that the oviduct may remain functional most of the year with the accompanying possibilities of increased length of infection.

In conclusion, it is to be especially noted that the bursa Fabricii appears to be the more normal host structure for supporting the existence of *Prosthogonimus;* that in nature, young birds may serve as reservoirs for these flukes; but where atrophy of the bursa occurs, these parasites are supported only in the oviduct and for a relatively brief time due to the short functional season of that structure.

Immunity.—Hens B242 and B2074 were fed *Prosthogonimus* cysts April 20 and they responded to infestation by exhibiting marked reduction in egg production. Fecal examination (altho not entirely reliable for diagnosis of the presence of these flukes) indicated the loss of worms at the end of a relatively short period of time, and the birds were reinfested on September 18. Large examples of *P. macrorchis* were taken from these birds on October 15 and 18, respectively, indicating that hens are subject to reinfestation during the same season.

In all cases where two feedings of an approximately equal number of cysts each were given a few days apart, the second feeding always resulted in considerably less numbers of the parasites than the first, and such examples showed a slower rate of growth. Hen M1737 was fed 60 cysts April 7, and another 45 on April 17. As a result of these feedings, 32 large and two very small *P. macrorchis* were collected on April 24. The crow, fed five *Tetragoneuria* naiads May 25 and ten such naiads May 30, produced seven large and one small *P. macrorchis* on June 10. The English sparrow, given ten *Prosthogonimus* cysts on July 19 and ten more July 23, yielded eight mature and two very small specimens of this trematode. Therefore, during the time that birds

[3] In rare cases, *Prosthogonimus* has been found in the oesophagus, cloaca, and intestine.

are infested with *Prosthogonimus,* they tend to be partially immune to further infestation with such parasites.

Hatching experiments.—Eggs of *P. macrorchis* were obtained March 2, 4, and 5, 1933, and were kept in containers as indicated in the section dealing with technic. Examinations were made at three-day intervals during a six-weeks period but no hatching took place. As soon as snails could be obtained they were kept in small containers to which quantities of eggs, obtained after the method of Krull, 1931, had been added. Examples of *Amnicola, Lymnaea, Physella, Gyraulus, Stagnicola, Fossaria, Helisoma trivolvus, H. antrosa,* and *H. campanulata* readily ate the eggs, but neither miracidia nor hatched eggs could be found. All of the numerous eggs in the feces of the snails, even in the case of *Amnicola,* still retained the operculum.

As viewed inside of the mature egg in the condition found in sections of the metraterm, the miracidium appears to be in the mature condition, or nearly so.

Cercaria

An intensive survey of Glenwood Lake, made during the summer and fall of 1932, yielded the following genera of molluscs: *Physella, Lymnaea, Amnicola, Gyraulus, Helisoma, Fossaria, Sphaerium, Anadonta,* and *Ancylus.* With the others found in the spring of 1933, these molluscs were examined for parasites and a wide range of types of cercaria was found. It was expected that the body of the cercaria of *Prosthogonimus macrorchis* would be large and similar to that illustrated by Szidat, 1926, as that of *P. pellucidus.* According to his description, the cercaria he found was 0.5-0.7 mm. in length, 0.15-0.25 mm. broad, and bore a stylet. It is very doubtful if this was a cercaria of *Prosthogonimus,* since that of *P. macrorchis* has a length of only one-fourth to one-fifth that of his type. He figured for his species an excretory bladder much more prominent than that of *P. macrorchis.*

In view of Szidat's description, altho the writer had seen and figured the real cercaria of *Prosthogonimus,* during the middle of the summer of 1933, most of his attention was given to larger cercaria, none of which would infest the naiads. Meanwhile, Mr. W. W. Crawford, searching for the cercaria of a frog trematode, obtained infestations in naiads with the small cercaria from *Amnicola limosa porata* (Say). He very kindly called my attention to the fact that there was a close resemblance between the young metacercaria formed and the small metacercarial types which accompany infestation with *Prosthogonimus* cysts. A survey in 1932 and 1933 of several lakes of the Twin City region had shown that the adult and nymphal dragonflies of Lake Johanna were free from *Prosthogonimus* infestation. The writer dissected 74 adult *Tetragoneuria* and over 500 naiads of this genus and of *Epicordulia, Mesothemis,* and *Leucorrhinia* without finding a single cyst of this trematode group, so if they did occur, they were present in very small numbers.

One half-grown *Leucorrhinia* and 29 partially-grown *Epicordulia princeps* naiads from Lake Johanna were distributed among 10 water-filled finger bowls, following experimental infestation with the small cercaria (Plate VI, Fig. 2) from *Amnicola limosa porata* taken from Glenwood Lake. As controls, over 200 naiads of *Epicordulia* and *Leucorrhinia,* collected from Lake Johanna at the same time the experimentally-infested naiads were taken, were kept in containers near the infested group, and part of this number was dissected from time to time, always with negative results.

The small cercaria of *P. macrorchis,* which develops in the snail *Amnicola limosa porata,* were placed in Syracuse watch glasses containing one to three naiads and the respiratory currents served to draw them into the anus of the naiads. Movements of the cercaria were not directional, the lashings of the tail merely serving to lift the cercaria from the bottom of the watch glass. Therefore it appears that the cercaria is not attracted by the host except as it is drawn inside by breathing movements of the naiad. Often a cercaria would touch various parts of the dragonfly body and would immediately attach by its suckers and crawl over the surface with leech-like movements, but entry was always passive, none ever having been seen to enter by boring through the chitinous covering. Frequently the anal setae would hinder the passage of the worm, and sometimes the naiad would sense the obstruction and try to expel it with violent spurts of water. Strangely enough, however, once a cercaria had been drawn inside, it rarely came out again. Various other kinds of cercaria were invariably expelled after passive entrance through the anal opening.

Habits of *Amnicola limosa porata* (Say)

During the period between August 14 and November 5, 1933, 1,227 specimens of *Amnicola limosa porata* were examined for cercarial infestation and of these 2.7 per cent were infested with *Prosthogonimus* sporocysts and cercaria. Altho the amount of infestation steadily declined during the period of examination, snails with this cercaria were found as late as November 5, which approached the time of freezing of the lakes of the Minneapolis region.

Amnicola limosa porata (Plate VIII, Figs. 7 and 8), measuring less than three millimeters in length and very retiring in its habits, is among the smallest of the snails of the lakes in the vicinity of Minneapolis and is very easily overlooked. The writer first saw numbers of this snail in Glenwood Lake in the fall of 1932, where it was frequently found on the undersides of submerged boards and sticks, in company with *Gyraulus parvus,* a small, discoidal snail. Frequently *Amnicola* travels on the lake bottom, where it may be observed in quiet situations. Such a habit would facilitate the eating of *Prosthogonimus* eggs, a point of importance if the eggs must be eaten to hatch, as is the case with certain other trematode eggs. Large numbers of *Amnicola* occur on *Chara, Elodea,* and other aquatic vegetation on which they can hide among the compact foliage. Numbers may also occur on decaying, matted plant stems.

Most of these snails are not found in extremely shallow water, but occur farther out where the depth ranges from one to two feet or more. As in the case of the dragonfly hosts, there is a tendency for numbers to collect in one area, perhaps due to favorable ecological factors. As the temperature of the water rises, the snails seek shaded areas, a fact which may account for the heavier infestation in such places of dragonflies with *Prosthogonimus. Amnicola* became scarce during the middle of the summer of 1933, possibly due to the heat, cercarial infection, or to both.

This species of *Amnicola* "is common in the lakes of Michigan, Wisconsin, Minnesota, and other northern parts of the United States," according to Dr. F. C. Baker (personal communication).

Metacercaria

Identification experiments.—Altho Kotlan and Chandler, 1927, showed that the striated cysts from dragonflies of Muskegon, Michigan, contained the metacercaria of what is now designated *P. macrorchis,* they did not determine the dragonfly hosts. Lakela, 1931, found in her experiments that this fluke was developed by feeding cysts occurring in *Tetragoneuria* in Minnesota.

Results of a survey in 1932 and 1933 on the *Prosthogonimus* cysts of both adult and nymphal dragonflies of Minnesota, especially in the Twin City area, revealed four genera of dragonflies as hosts,[4] as follows: *Leucorrhinia, Tetragoneuria, Epicordulia,* and *Mesothemis* (= *Erythemis*). To determine whether the metacercaria represented one species or more, cysts from each type of dragonfly were fed to domestic ducks, and there was produced in the bursa Fabricii in each case the typical form of *Prosthogonimus macrorchis.*

In addition to the colorless, clear *Prosthogonimus* cysts, there were found in naiads of *Tetragoneuria* and *Epicordulia* brown cysts of nearly

[4] Identified as *Leucorrhinia intacta* Hagen, *Tetragoneuria cynosura* Say, *T. spinigera* Selys, *Epicordulia princeps* Hagen, and *Mesothemis simplicicollis* Say.

the same size as the others. Such cysts contained metacercaria identical in appearance to those of the former. Some of these were fed to a laying hen, K328, with the result that there was produced in the oviduct the same species of fluke, the individuals of which were usually large. One such specimen was taken in a living state from the egg-white of the same hen during the period of infestation. These flukes, aside from their large size, exhibited vitelline fields which hardly more than reached the testes. In this respect they resembled the condition found in a fluke taken from a hen's egg at Hines, Minnesota, July 5, 1933, in which the vitellaria even failed to reach the anterior margins of the testes. In addition, the cirrus sac of this specimen was unusually long, and the uterus in the posterior part of the body showed a minimum of coiling. Brown cysts, which produce the large form of *P. macrorchis,* did not occur in naiads belonging to *Leucorrhinia* or *Mesothemis*.

Second intermediate hosts of *P. macrorchis*.—Aside from the dragonfly hosts mentioned in the preceding section, naiads of *Libellula luctuosa* in a few instances contained what appeared to be partially developed cysts of *Prosthogonimus,* but when they were fed to ducks no flukes were produced. This may mean that this dragonfly is a "border-line" host. It is to be recalled that another member of the genus, *L. quadrimaculata,* is a normal European host of *P. pellucidus*. No cysts of the trematode under consideration were found in *Gomphus, Pachydiplax, Sympetrum,* or *Anax* from the investigated lakes, and none were detected in numerous naiads taken from Glenwood Creek and the St. Croix River, altho other trematode cysts did occur in them.

Considering now the dragonflies of Glenwood Lake, *Leucorrhinia* naiads were heavily infested, the infestation averaging 10.4 cysts each. A single specimen yielded 90 mature cysts, while some had 60 or 70 and many had slightly less. It is to be noted that naiads taken from the south and east side of the lake, where the ducks stay most of the time because of extra food furnished them by picnickers, have much greater infestation than those from the north end, the latter frequently being free from cysts. There is an average of 8.4 cysts each for *Tetragoneuria,* 11 each for *Epicordulia,* and only 0.29 each for *Mesothemis*. With its two-year cycle, *Epicordulia* is exposed to infestation more times than the others, and the large naiads do have a heavier infestation than the younger naiads in this genus.

In 1926, Szidat reported that the dragonfly *Libellula quadrimaculata* and *Gomphus* sp. carry *P. pellucidus,* and he later (1931) added *Cordulia aenea* to the host list of this species. Of 100 naiads of the latter species he found 74 per cent infested with *Prosthogonimus* cysts and these contained 975 cysts. The infested naiads had from 1 to 72 cysts each and this quantity indicates a close similarity between the average infestation of the dragonflies of this German lake (Dammteich) and of Glenwood Lake, Minneapolis.

Later, Ono, 1930, examined about 100 *Anax parthenope* found in the vicinity of Mukden, South Manchuria, and found about 30 cysts of *P. putschkowskii,* so determined by him by feeding them to a male fowl. He found no *Prosthogonimus* cysts in more than 300 other dragonflies belonging to two species of *Sympetrum* and one species of *Orthetrum.*

Habits of dragonfly hosts of *P. macrorchis.*—Differences in the habits of dragonfly hosts must be taken into account when considering the factors entering into the extent and periodicity of prosthogonimiasis as has been well illustrated by the studies of Szidat, 1931, already discussed. The following observations made by the writer over a period of nearly two years, while far from complete, nevertheless show various differences in behavior.

The naiads of *Leucorrhinia* are found clinging to plants which form matted beds, and may be close to shore or as much as 50 feet or more out from the shore. They are common, active insects which collect along the shore previous to the general emergence, during the last of May and the first of June. They do not seem to occur in ponds or very small lakes, as they have been found only in medium-sized or large lakes with the proper vegetation mats. Adults of this genus are the common, small, black-bodied, clear-winged dragonflies with white "faces."

Naiads of the genus *Tetragoneuria* commonly occur on a rather firm, sandy bottom or muddy bottom, where they live among the trash or vegetation and are often found in the cracks of submerged sticks and logs, and among the root-masses of aquatic plants, but do not live up among the foliage of the vegetation as is the case with *Leucorrhinia.* They have a slow-moving gait while they are walking but they swim with considerable rapidity, as can the naiads of the other groups discussed here, by spurting water from the anus while holding the forelegs forward. The adults are very curious, hovering dragonflies, which spend most of their flying time darting with lightning rapidity from place to place. Strangely enough, they appear in numbers in the late afternoon between four and six o'clock and adults were not seen at other times, except in the case of freshly emerged individuals.

Largest of the groups here considered are the dragonflies of the genus *Epicordulia,* of which *Epicordulia princeps* is our species. Like those of *Tetragoneuria,* the nymphs "sprawl" on the trash of the hard sandy or muddy bottom, often among vegetation. Due to a two-year life cycle, they are exposed to a double amount of infestation. The adults are high and swift fliers and are almost impossible to capture with a net.

Smallest of the four genera are the short, thick-bodied and golden-eyed naiads of *Mesothemis*. Less common in numbers and carrying slight infestation, they are not of great importance as hosts of *Prosthogonimus*. The nymphs are frequently found clinging to vegetation, and are quite active. The green-bodied and clear-winged adults are easily recognized, and because of their habit of resting on low herbage along the shore, they are quite easily captured. Ovipositing females glide along close to shore just above the water and periodically tap the surface with the tips of their abdomens.

Very young naiads of these groups were seen first on July 1, and the first occurrence of *Prosthogonimus* in them was noted July 7, altho early stages of the metacercaria were found abundantly in year-old *Leucorrhinia* on July 7.

Naiads of *Mesothemis, Tetragoneuria,* and *Leucorrhinia* are exposed to *Prosthogonimus* cercaria during the summer and fall of one year and are again exposed to infestation the following spring, prior to their emergence. After the ice coat had formed, holes were cut in it from time to time to inspect winter conditions. In early December, when there was a foot of ice on Glenwood Lake, nymphs of *Leucorrhinia* and *Tetragoneuria* were taken from the blanched vegetation and mud in the small amount of water remaining at that point. On March 29 of the following year (1933), holes five feet square were again cut through the ice, which was just beginning to thaw, and a number of *Tetragoneuria* naiads were obtained. All of the dragonfly naiads taken from the lake in the winter contained about the same amount of infestation as did those examined in the fall.

At the time of general emergence, which takes place during the latter part of May and the early part of June, hordes of dragonfly naiads of the above groups collect along the shallow water's edge, climb up some convenient plant stem and transform. This period provides an excellent time for many kinds of birds to gorge themselves on the insects and, in so doing, allow for the completion of the *Prosthogonimus* life cycle. It is not only the naiads which are eaten at this time by birds, but the adults also are devoured in quantity. Needham and Heywood, 1929, state, "The birds that most habitually eat Odonata and that capture them in flight are the swifts and swallows . . . the bird that is most often seen deliberately selecting individual dragonflies for capture is the kingbird . . . the smaller hawks, shrikes, cockoos, and flycatchers also eat dragonflies, only less openly. The bee-eater, *Merops persicus,* is said to capture dragonflies with the sole purpose of using the wings as lining for his nest." As previously mentioned, Dr. Riley saw English sparrows feeding nestlings with dragonflies.

Position of the cysts in the body of the host.—For the purpose of determining the location of the cysts of *Prosthogonimus* within the body of the host, 14 naiads of *Leucorrhinia* taken from Glenwood Lake in the fall of 1932 were carefully dissected and the positions of the cysts noted. A total of 162 of these cysts was distributed as follows:

Posterior half of abdomen................	109
Anterior half of abdomen................	43
Thorax	6
Head	4

This uneven distribution is easily explained on the basis of the portal of entry of the cercaria, which is the anal opening. The path of least resistance from there would undoubtedly be through the branchial basket to the ventral muscles of the posterior part of the abdomen.

On a number of occasions, cysts were found in the coxae. In the head they were seen on the labium, in the region of the brain, and even in the eye, in one case. Ono, 1930, reported a similar case of a cyst of *P. putschkowskii* in the eye of *Anax parthenope*. It is interesting to note that cysts of *P. macrorchis* did not occur on the labium unless there was a total of 20 or more cysts in the body, and the occurrence of two or more cysts on the labium was found to be a sure indication that the naiad was even more heavily parasitized. It was also noted that no cysts were ever found in the heads of any of our dragonflies except *Leucorrhinia*.

In most instances cysts are found in the ventral part of the body, but they also occur in the dorsal part, where they are held by muscular tissue or trachae. It cannot be said positively that any are actually free in the body cavity altho they are frequently attached very insecurely.

Longevity of cysts in artificial media.—When *Prosthogonimus* cysts are removed from the hosts and placed in water, the metacercaria are active at first, but after an hour or so gradually become quite opaque and the metacercaria die. This point is of particular interest since it is sometimes necessary to transport living cysts from one location to another when feeding experiments are in progress, causing a delay which might prove fatal to the metacercaria and render the results unreliable.

In 0.7 per cent NaC solution several groups, each of 20 cysts with living metacercaria, were observed from June 7 to June 10 to ascertain their ability to live in this medium. Examinations were made by pinching the cysts with a pair of forceps and watching for movements of the metacercaria. At the end of the period the trematodes seemed as viable as at any time before.

The process of excystment.—Near the close of the longevity experiment some metacercaria were seen to have emerged, an observation which indicated that they were able to escape from the tough sheath by their own action. Another group of 24 cysts was placed in 0.7 per cent saline solution and after 48 hours six metacercaria had escaped and all were actually moving about the container, while several other worms still inside of the cysts were moving about rapidly in the same manner as those placed in digestive juice. It is possible that the penetration of the cyst wall may be accomplished with the aid of numerous gland cells located anterior to the ventral sucker and whose ducts lead forward (Plate VIII, Fig. 2).

To obtain metacercaria for study purposes, cysts were placed in an alkaline solution of tryspin. About one-half minute had elapsed before the metacercaria began to move about rapidly. From this time until their release they remained in a more or less continual state of feverish activity. The thin membrane surrounding the cyst first "blistered," leaving a space between it and the remainder of the wall, after which the inner layer of the wall was digested in a period of from 30 minutes to several hours. When the inner wall had been digested away, the worm alternately attached its oral and ventral suckers to the wall which it pushed and pulled with frantic efforts.

The cyst cavity was now filled with liquid and excretory granules which the trematode had expelled from the bladder. Finally, the worm punctured the wall and the metacercaria left, always oral end first, and this last effort was often one of considerable difficulty. There is much difference in the time of excystment even under the same conditions, but higher temperatures and increased strength of digestive juice will greatly hasten the process. Merely placing the cysts in water made alkaline with sodium carbonate will cause a similar response on the part of the worm, finally resulting in its release.

Development of the metacercaria in naturally-infected naiads.—Sections indicate that after its entrance into the host the metacercaria always becomes located in the muscle, especially the ventral abdominal muscles (Plate VII, Fig. 6). The width of the youngest metacercaria found was 100 μ and this dimension was more than doubled by the time of the formation of the secondary cyst-wall elements. In all of the sections, the Y-formed excretory bladder with its heavy walls is a prominent structural feature. Intestinal ceca (Fig. 6, in) are seen in the earliest stages, and by the time the diameter reaches 200 μ, primordia of the testes appear. A membrane is very early thrown around the parasite. Undoubtedly the metacercaria grows by nutriment derived from the muscular tissue of the host, and numerous gland cells located beneath the cuticula of the trematode may secrete a digestive fluid.

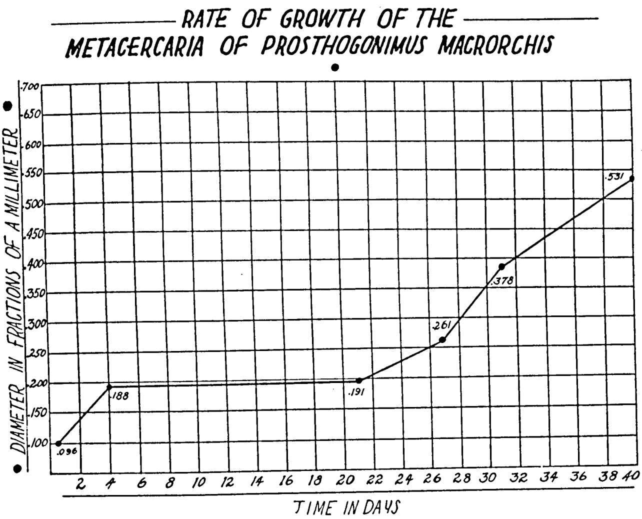
Broken muscle fibrillae indicate the destructive activities of the invader, which is oriented within the muscles in such a way that its longitudinal axis is parallel with the direction of the muscle fibrils, which become considerably spread apart by its body.

Rate of growth of the metacercaria.—Following experimental infection of naiads of *Tetragoneuria spinigera* Selys with the cercaria of *Prosthogonimus,* dissections of dragonflies at intervals and recovery of young metacercaria furnished data on the rate of growth under laboratory conditions. After a period of 16 hours, the young metacercaria, 0.096 mm. long, had reached the ventral abdominal muscles but still retained the stylet (Plate VII, Fig. 1). When the next metacercariae were observed, four days after the entrance of the cercaria, the stylet had been lost and the body size had doubled. At the end of 40 days the body had reached a size in which the diameter of more than one-half millimeter was over five times the same dimension of the youngest observed stage. Growth rate (Graph 1) is seen to have been greatest during the first few days, followed by a long period of little growth, and finally a sharp increase in rate. Two naiads dissected on December 16, 66 days after infection, produced five and three matured *Prosthogonimus* cysts, respectively, and these exhibited all of the characteristic features of the metacercaria of *P. macrorchis,* enclosed in its radially-striated, thick-walled cyst. One cyst did not show the thick wall but it was developed in all of the others. In the latter, the walls were at approximately the same stage of growth. The average diameter of the seven matured cysts was 0.432 mm. and the wall was 0.054 mm. in thickness. The naiads producing these cysts measured about 14 mm. long. All of these experimentally-reared cysts containing active metacercaria were fed to hen C277, pen-reared at the University Farm and in laying condition. Ten days later she was killed, but unfortunately the oviduct had receded to the completely resting condition and no trematodes were found.

Of two larger naiads, (*Epicordulia princeps* Hagen) about 18 mm. long, one infested with *Prosthogonimus cercaria* for 67 days was dissected December 30, 1933, and 20 *Prosthogonimus* cysts with the typical striated walls were removed from the abdomen and fed to Hen C278 and C2190, the cysts divided evenly between them. On January 1, 1934, the other naiad infested for 69 days was found to contain 13 cysts of *Prosthogonimus,* but these had thinner walls, altho they were sufficiently thick to show clearly the striated condition. These cysts were fed to Hen C278 on the same day.

Both of the hens were killed on January 13, but no trematodes were found. The cysts were undoubtedly not infective. The fact that the walls of the cysts were more or less soft and flabby, even tho striated.

and the fact that some of the metacercaria soon became more or less opaque (a sign of death) after they were removed from the dragonfly, indicated that their vitality was low.



Graph 1

There is no doubt but that the cysts experimentally developed were those of *Prosthogonimus,* since they were morphologically indistinguishable from the peculiar cysts known to belong to that genus, and since the cercaria which produced them came from Glenwood lake where the dragonflies are infested with cysts which produce *Prosthogonimus.*

PROSTHOGONIMUS DISEASE (PROSTHOGONIMIASIS)

Economic Importance

In *Prosthogonimus* infestation we are dealing with a poultry problem of the first rank, particularly in the lake districts of the world, but one in which the economic importance is just beginning to be realized. Its effects have been observed for centuries by farmers in Europe, but only recently (Hieronymi and Szidat, 1921) has it been found that it is due to the presence of flukes, which in Europe have been found to be *P. pellucidus* von Linstow (= *P. intercalandus* Szidat, 1921), a species found in the oviducts of domestic fowls in that region.

Thienemann, 1920, noticed the correlation between the extensive flights of the dragonfly *Libellula quadrimaculata* and the production of soft-shelled eggs by domestic hens. Szidat, 1926, proved that *P. pellucidus* developed from cysts with radially-striated walls, from *L. quadri-*

maculata. In 1931 the same author implicated the dragonfly, *Cordulia aenea,* as another intermediate host of that trematode.

According to Szidat, 1927, during the spring of 1926 it was impossible to obtain fresh eggs in the vicinity of Rossiten, in East Prussia, due to the devastating effects of *Prosthogonimus* disease, and if a hen harbored more than forty or fifty of the flukes she usually died. The same author, 1933, refers to this trouble as the most important disease of the lowlands of the Northern Hemisphere. Rheinhardt, 1922, Seegart, 1923, Mass, 1923, and others have reported it from various sections of Germany. De Blieck and van Heelsbergen, 1923, reported quite similar trouble for Holland, and also indicated *P. pellucidus* as the cause. In North America, Kotlan and Chandler, 1925, found that a serious poultry disease at Duck Lake, Michigan, was due to an undetermined fluke of the genus *Prosthogonimus.*

Our studies have extended the work of others and have shown that the infestation is widely prevalent in the United States and is due to a new species, *P. macrorchis,* which is related to *P. pellucidus* but distinct from it.

Effect on egg production.—European workers have stated that one of the principal detrimental effects of *Prosthogonimus* disease as caused by *P. pellucidus* was the decrease in egg production. To determine the effect of such an injury which might be due to *P. macrorchis,* the writer undertook experiments upon laying hens. Through the courtesy of Dr. F. B. Hutt, to whom we are obligated for many favors, a flock of 16 white-leghorn hens with known laying records were selected from birds kept by the poultry division of the University of Minnesota. Since they had been reared in pens far from any lake and were producing eggs in a normal manner, they were evidently free from *Prosthogonimus* infestation. The hens were cared for by their regular attendants, and the usual trapnest egg-records were kept during the course of the experiments. On April 20, 1933, eight of the hens were fed cysts of *Prosthogonimus* from naiads of Glenwood Lake (Table 7), and the other half were kept as controls in the same pen. The records of four hens, two from each group, which died during the experiment, were not used since it was evident that their deaths were due to causes other than *Prosthogonimus* disease.

During the third week in April the hens which were later infested with *Prosthogonimus* averaged 5 eggs each and the control hens averaged 5.2 eggs each, so that egg production in the two groups was nearly equal at the beginning of the experiment. Beginning with the last week in April there was a tremendous drop in egg production of the treated hens as contrasted to a slight drop in the control group's laying record. The controls averaged 3.9 eggs each per week for the first half of May in contrast to the strikingly low average of 0.4 egg per hen during the same period. During this time the controls laid nearly ten times as many eggs as did the birds infested with *Prosthogonimus!* In spite of the fact that the infested birds partially regained their previous laying average, they did not again reach their former high level. Four of the infested hens ceased laying a week after they were infested and did not lay a single egg during the first half of May.

Table 7

Egg Production Experiment

Fed cysts of *Prosthogonimus* April 20, 1933	No. of cysts fed	April Week 1	April Week 2	April Week 3	April Week 4	May Week 1	May Week 2	May Week 3	May Week 4	June Week 1	June Week 2	June Week 3	June Week 4
Treated hens													
B233*	75	0	4	3	1	1	4	0	0	.	.	.	.
B242	320	6	6	7	4	1	1	4	1	3	3	4	0
B2013	50	3	6	2	0	0	0	0	1†	.	.	.	.
B2029*	25	3	1	7	3	1‡	.	.	.	.	.	.	.
B2071	5	5	6	7	4	0	0	0§	.	.	.	.	.
B2074	15	4	4	4	4	1	2	6	6	3	1	0	0
B2038	100	2	3	3	0	0	0	4	5	1	3	2	3
B125	200	5	6	7	2	0	0	3	5	2	2	5	3
Total		22	26	30	14	2	3	17	17	9	9	11	6
Average		3.7	4.3	5	2.3	0.3	0.5	2.8	4.2	2.2	2.2	2.7	1.5
Control hens													
B219‖		.	.	.	.	.	.	.	.	.	.	.	.
B220		1	4	4	5	5	1	6	6	7	3	5	1
B245		6	5	1	0	0	3‖	.	.	.	.	.	.
B2004		6	7	6	3	6	6	7	7	4	6	4	4
B2052		5	5	6	4	4	2	4	7	4	6	3	3
B2054		3	6	5	1	2‖	.	.	.	.	.	.	.
B2057		4	6	5	5	4	4	5	4	4	4	0	0
B228‖		.	.	.	.	.	.	.	.	.	.	.	.
Total		16	22	21	17	19	13	22	24	19	19	12	8
Average		4	5.5	5.2	4.2	4.7	3.2	5.5	6	4.7	4.7	3	2
Control hens	Total	16	22	21	17	19	13	22	24	19	19	12	8
	Average	4	5.5	5.2	4.2	4.7	3.2	5.5	6	4.7	4.7	3	2
Treated hens	Total	25	27	30	14	2	3	7	17	9	9	11	6
	Average	4.1	4.5	5	2.3	0.3	0.5	2.8	4.2	2.2	2.2	2.7	1.5

* Records of B233 and B2029 not averaged in.
† Soft-shelled egg.
‡ Died.
§ Killed May 24.
‖ Died, eggs not counted.

Table 8

Results of *Prosthogonimus*-Cyst Feedings to Domestic Hens

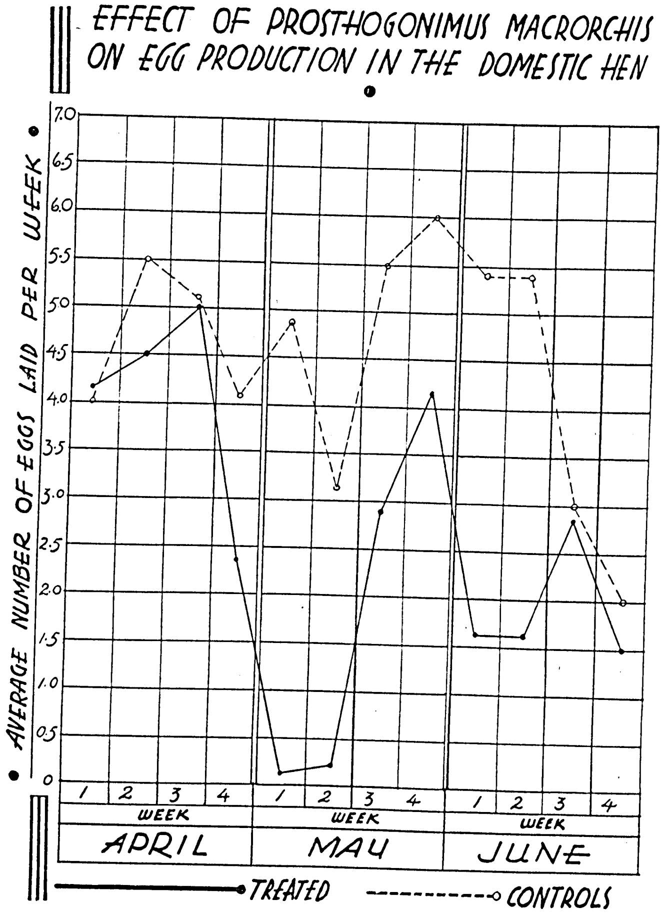
Chickens fed	Cysts or naiads fed	Date fed (1933)	Date killed (1933)	*Prosthogonimus* found	Age in days	Results
B1928	22 cysts (*Epicordulia*)	July 14	Aug. 4	14	21	Laid egg with live fluke, fluke large
K328	110 cysts	July 14	Aug. 14	1	31	Oviduct semi-functional, fluke large
B218	35 cysts	Sept. 18	Oct. 30	0	42	Oviduct resting
B2041	50 cysts	Sept. 18	Oct. 8	0	20	Oviduct resting
B2074	50 cysts	Sept. 18	Oct. 8	1	20	Fluke very large, see plate
B242	45 cysts	Sept. 18	Oct. 14	3	26	Flukes very large
B191	45 cysts	Sept. 18	Oct. 8	0	20	Oviduct resting
B2004	50 cysts	Oct. 15	Oct. 30	4	15	Oviduct functional but small
B2057	50 cysts	Oct. 15	Oct. 30	0	15	Oviduct resting
B752	161 cysts	Oct. 26 ('32)	Nov. 20 ('32)	0	25	Oviduct resting
B941	2 naiads (*Tetragoneuria*)	Nov. 27	Dec. 11	0	14	Oviduct resting
B737	5 naiads "	Dec. 8	Jan. 3 ('33)	0	26	Oviduct resting
B782	5 naiads "	Dec. 13 ('32)	Jan. 23	10	41	
B373	5 naiads (*Leucorrhinia*)	Feb. 15	Mar. 4	12	17	Laid soft-shelled egg
B369	5 naiads (*Tetragoneuria*)	Feb. 15	Mar. 4	15	17	Calcium deposits in body cavity
M1737	60 cysts (*Leucorrhinia*)	Apr. 7	Apr. 24	32	17	Laid soft-shelled egg, April 23, 1933
B2014	10 naiads "	Apr. 7	Apr. 24	7	17	Laid egg with live fluke, fluke large
B2071	5 cysts "	Apr. 20	May 24	0	34	
B2013	50 cysts "	Apr. 20	May 24	1	34	Fluke large

Table 9

Results of *Prosthogonimus*-Cyst Feedings to Domestic Ducks

Ducks fed	Cysts or naiads fed	Date fed (1933)	Date killed (1933)	*Prosthogonimus* found	Age in days	Results
C1481	10 naiads (*Leucorrhinia*)	May 20	Sept. 23	2	126	Found in the bursa Fabricii
Duckling						
C1480	10 naiads (*Tetragoneuria*)	May 20	Sept. 23	0	126	
C1479	15 cysts (*Leucorrhinia*)	May 24	July 1	2	36	Found in the bursa Fabricii
C1482	16 cysts (*Tetragoneuria*)	May 24	July 1	2	36	Found in the bursa Fabricii
L01	66 cysts (*Epicordulia*)	May 31	July 18	9	48	Found in the bursa Fabricii
L02	34 cysts (*Epicordulia*)	May 31	July 13	0	43	
L11	6 cysts (*Mesothemis*)	June 1	July 8	2	37	Found in the bursa Fabricii
L10	20 cysts (*Libellula*)	June 15	July 31	0	46	
L486	50 cysts (*Tetragoneuria*)	Oct. 2	Nov. 6	0	35	No bursa Fabricii
Duck						
L10001	140 cysts (*Leucorrhinia*)	Oct. 2	Nov. 6	0	35	No bursa Fabricii
C10002	140 cysts (*Leucorrhinia*)	Oct. 2	Nov. 6	0	35	No bursa Fabricii
C10003	14 cysts (*Leucorrhinia*)	Oct. 2	Nov. 6	2	35	Found in the oviduct

The striking fall in egg production (Graph 2) on the part of the infested group appears to be due entirely to *Prosthogonimus macrorchis,* since the control group showed no comparable drop. From previous feeding experiments it was found that worms may mature in a week and therefore could be expected to begin their disturbance by that time. The fact that the worms are usually lost between the third and fifth weeks would explain the rapid increase in production thereafter. Therefore it may be concluded that *P. macrorchis,* even when present in small numbers, causes a great amount of loss to poultrymen when their hens are allowed to become infested.



Graph 2

The occurrence of *Prosthogonimus* in eggs.—An interesting if not serious aspect of the problem is that living flukes may occasionally be found inclosed within the shell of otherwise perfectly normal eggs. Such occurrences have been reported by Braun, 1901a, Wolffhügel, 1906, Skrjabin, 1911, Khaw, 1930, Du and Williams, 1930, Shen, 1931, and others. Linton, 1887, identified as *Prosthogonimus ovatus* a large trematode from a hen's egg laid at Beloit, Wisconsin. He recognized that the description did not fit that of *P. ovatus* in certain respects and a comparison of his measurements with those of *P. macrorchis* clearly shows that he was dealing with the latter species.

It is probable that most cases of trematodes in eggs go unobserved or, at least, unreported. As is the case with *P. ovatus, P. japonicus,* and other species, there have been in the United States and Canada various instances of the occurrence of specimens of *P. macrorchis* in hens' eggs. Dr. Riley (unpublished data) received specimens of this parasite taken from eggs in Ontario, Canada. In that province the farmer who owned the hens infested with *Prosthogonimus* was boycotted because the eggs he sold contained considerable numbers of this fluke.

Mrs. M. D. Stoner of Hines, Beltrami County, Minnesota, sent in a living specimen of *P. macrorchis* which she had taken from a hen's egg on July 5, 1933. Shortly after this, two living specimens of the same species of fluke, taken from hens' eggs, were sent from the North Central Experiment Station of the University of Minnesota, at Grand Rapids, Itasca County. Superintendent Donovan of that station, in a personal communication, stated that the farmer whose hens produced the infested eggs lived on the edge of a large lake, 18 miles south of Grand Rapids. On August 9, three eggs opened for supper contained the flukes. Of significance in this case was the fact that the farmer claimed that he had kept his hens shut up and that all the water they drank came from a well. In this case, infestation either came from allowing the hens access to the lake-shore at some previous time that season, or adult dragonflies settled in the hen-yard and the hens ate them.

On August 2, a living example of *P. macrorchis* was found in the white of an egg laid by hen B192, which had been fed 22 large brown cysts July 14. In another egg from an experimentally-infested hen a distorted and smaller specimen was found compressed on the surface of the yolk. A string of the characteristic eggs leading from the region of the oral sucker confirmed the identification.

It is not hard to understand the phenomenon of the enclosure of *Prosthogonimus* in bird eggs when one considers that these parasites of the oviduct are continually on the surface which secretes the egg materials.

Histological Pathology

Sections of the oviduct of Hen B2074 showed the presence of large numbers of plasma cells. Secretion granules were present in large numbers in the columnar epithelial cells of the mucosa of the uterus. Relatively few eosinophiles were present in the oviduct tissue. The normal oviduct, as illustrated in detail by Surface, 1912, does not show the presence of plasma cells.

Bittner, 1923, found infiltration of large numbers of plasma cells and eosinophiles into the tissue of the oviduct in cases of prosthogonimiasis, and Seifried, 1923, found that sections of the oviducts of such cases revealed the presence of many lymphocytes but few eosinophiles.

Diagnosis

Because of the somewhat obscure symptoms, especially in light cases of *Prosthogonimus* disease, there is a great probability of overlooking the trouble. On the other hand, caution must be exercised in diagnosis so as not to confuse this disease with other disturbances of the oviduct which occur, such as those which result from nutritional irregularities.

Positive diagnosis of prosthogonimiasis can be made from the presence of the mature trematode or from the finding of its characteristically-shaped eggs in the feces. Unfortunately, it is not always possible to determine the presence of this fluke by fecal examination of the fowl suspected of being infested. Seifried, 1923, and other workers have stated that they were not able to find eggs in the feces of infested hens, either by direct smear or by concentration methods. The writer was able to obtain several eggs in each of several direct smears from feces of hosts harboring from fifteen to thirty of the trematodes, but in other cases where fewer parasites were present, but enough to cause trouble, even extended examinations did not reveal the presence of eggs in the feces. It is probable that the eggs are discharged periodically, as there is not a constant passage of bulky material through the oviduct as there is through the intestine.

Aside from the certain diagnosis which can be made from the actual finding of the parasite or its eggs, the following symptoms in birds which have had access to the lake-shore when taken collectively are strongly suggestive of the disease produced by *P. macrorchis:*

1. Inactivity on the part of the hen.
2. Sharp decline in egg production.
3. The laying of soft-shelled eggs.
4. Presence of chalky-white crusts on the feathers around the cloacal region.

5. Distension of the abdomen in the cloacal region and bluish-red color of the skin of the abdomen (advanced cases).
6. Presence of hard, cream-colored chunks of abortive egg-white and yolk in the oviduct and abdominal cavity.
7. Distended oviduct filled with fibrinated pus, and abdominal cavity with pus-exudate, lesions, and peritonitis.

Prevention

Knowledge of the method by which this parasite reaches its final host, the hen, makes clear possible methods of preventing infestation. From comparative life-history studies of trematodes, and from investigations on the biology of the various species of *Prosthogonimus,* it may be stated without doubt that transfer of *P. macrorchis* to poultry is made through the young and adult forms of dragonflies only.

To prevent hens from becoming infested, it is advisable to keep them fenced away from the shores of lakes. This need not be done in the case of temporary ponds, or streams, for they have not been found to harbor the required species of intermediate hosts. Since young chickens may serve as reservoirs, it is essential that they also be kept from running near the lake, where their droppings would form a source of contamination. It is especially necessary that hens be closely confined during the peak of dragonfly emergences, which occur the latter part of May and the first part of June. Adult dragonflies are easily captured by poultry on damp mornings and for this reason the fowls should not be turned loose in the mornings until the dragonflies are out of the weeds.

Since crows and English sparrows have been shown experimentally to be capable of harboring mature examples of *P. macrorchis,* these birds probably serve in nature as reservoirs for this fluke. A reduction in the numbers of crows and English sparrows already has been deemed desirable for various reasons, and such a reduction would also tend to restrict prosthogonimiasis.

Treatment

According to Bunyea, Hall, and Cram, 1933, repeated doses of carbon tetrachloride in quantities of from 1.5 to 1.7 cubic centimeters of the drug, given in liquid cereal, have been reported as successful treatment for prosthogonimiasis. For treatment of liver-fluke infestation, the same medication has given fair results. Because of the toxic effect of this drug, care should be exercised in its use.

SUMMARY AND CONCLUSIONS

1. There is presented a historical resumé of facts about the genus *Prosthogonimus,* particularly from the biological and economic standpoints.
2. Included are methods of general survey work, care of experimental animals, and technic of the preparation of permanent mounts of material.
3. A diagnostic summary of the description of *P. macrorchis* is given, together with its differentiation from the other members of the genus, key for the separation of the species of the genus, taxonomic position of the genus, and a brief description of each species.
4. There is presented a detailed account of the gross and histological morphology of the adult, sporocyst, cercaria, and metacercaria of *P. macrorchis.* It was found that no redia form was present in the life cycle of this species.
5. The cercaria was found to be a typical xiphidiocercaria since it possessed a stylet and a short simple tail.
6. The Y-shaped, small excretory bladder was the only recognizable feature of the cercaria relating it to its adult form.
7. The flame-cell pattern of the species, as found in the living specimens, was $2[(2+2+2)+(2+2+2)]$.
8. An adult wild mallard-duck, with atrophied bursa Fabricii, could not be infested with *P. macrorchis.*
9. Examples of *P. macrorchis* in an experimentally-infested crow (*Corvus brachyrynchos*) matured in 17 days.
10. Eight out of 10 cysts of *P. macrorchis,* fed to an English sparrow (*Passer domesticus*), produced mature flukes in 14 days.
11. Two specimens of *P. macrorchis* were taken from a domestic duck 18 weeks after infestation.
12. Ducks are believed to be the normal hosts for *P. macrorchis* and the domestic hen is thought to be an abnormal host for it.
13. Hens lose their infestation of *P. macrorchis* in from three to five weeks.
14. *P. macrorchis* shows a tendency to considerable variation.
15. In general, the specific characters of *P. macrorchis* hold for specimens reared in the ducks, crows, chicks, and English sparrow, altho host modification was evidenced in each case.
16. Sucker ratio is the most constant of the specific characters, regardless of type of definitive host.
17. Habitat within the host has more influence on the variation of structure of *P. macrorchis* than does the kind of host.
18. Rate of growth of the marita of *P. macrorchis* is relatively slow in ducks and chicks but more rapid in the oviducts of hens.

19. Early loss of the bursa Fabricii in birds restricts the extent of *Prosthogonimus* infestation.
20. The bursa Fabricii appears to be a more normal habitat for *P. macrorchis* than does the oviduct.
21. A bird infested with *Prosthogonimus* tends to show partial immunity to further infestation.
22. Hens may be infested more than once during a season.
23. Eggs of *P. macrorchis* could not be made to hatch, even when fed to *Amnicola limosa porata*.
24. *Amnicola limosa porata* was found to be the first intermediate host of a species of *Prosthogonimus,* presumably *P. macrorchis.*
25. Dragonflies of the genera *Leucorrhinia, Tetragoneuria,* and *Epicordulia* were found to be important hosts of *P. macrorchis.*
26. Dragonflies of the genus *Mesothemis* carry *Prosthogonimus,* but only to a limited extent.
27. Individuals of *Leucorrhinia* carry the largest numbers of *Prosthogonimus* cysts. One naturally-infested naiad of this group was found to contain 90 mature cysts of this fluke.
28. Dragonflies of the genera *Anax, Pachydiplax, Sympetrum,* and *Gomphus* were found to be free from *Prosthogonimus* cysts.
29. Entrance of the cercaria of *P. macrorchis* into the dragonfly host is passive.
30. Habits of *Amnicola limosa porata* are discussed.
31. *Prosthogonimus* metacercariae in the dragonflies *Leucorrhinia, Tetragoneuria, Epicordulia,* and *Mesothemis* were all found to produce the marita of *P. macrorchis.*
32. Metacercariae from brown cysts were found to produce somewhat larger examples of *P. macrorchis.*
33. While occasional, small *Prosthogonimus*-like metacercariae were taken from naiads of the dragonfly *Libellula luctuosa,* such forms did not produce flukes when fed to a duck.
34. Dragonfly naiads of streams were not found to be infested with *Prosthogonimus* metacercariae.
35. Habits of the dragonfly intermediate hosts of *P. macrorchis* are discussed.
36. Cysts of this species of *Prosthogonimus* occur mostly in the ventral abdominal muscles of the posterior part of the abdomen and to a less extent in the other parts of the bodies of dragonfly intermediate hosts.
37. Living cysts of *P. macrorchis* remained viable in 0.7 per cent saline solution for more than three days.
38. The metacercaria of this species of fluke may escape from the cysts by its own action.

39. The metacercaria first invades the muscle of the host where it increases about five times in size before the striated wall forms.
40. The stylet of the cercaria is retained for a short time after entry into the dragon host.
41. The ventral sucker of the cercaria and youngest metacercaria is about one-half smaller than the oral sucker, while this size-ratio is reversed in the marita.
42. The growth rate of the metacercaria was found to be greatest during the first few days and during the last half of the period of size-increase, with an intervening pause during which almost no growth took place.
43. Summarizing the life cycle of *P. macrorchis,* the sporocyst, found in the "liver" of *Amnicola limosa porata,* produces the cercaria directly, there being no redia stage. The cercaria swims away from the snail-host, and, if it is drawn into the anal opening of a suitable species of dragonfly naiad by the breathing movements of such a host, the tail of the cercaria is lost and the metacercaria thus formed makes its way to the muscle of the naiad, where it increases to about five times its original size. A thick wall with an outer radially-striated and an inner homogeneous layer now forms about the metacercaria and the cyst usually comes to lie in the body cavity of the host. In the event the infested dragonfly naiad or adult is eaten by a suitable avian definitive host, the wall is digested off the cyst as it passes down the digestive tract of the bird. The worm then makes its way down the intestine to the cloaca and then to the bursa Fabricii or the oviduct, where it develops into the mature trematode. Embryonated eggs produced by the fluke leave the host by way of the cloacal opening, and if they reach a lake inhabited by *Amnicola limosa* the latter becomes infested and sporocysts and cercariae develop.
44. *P. macrorchis* produced a striking fall in egg production in hens infested with it. One group of hens laid an average of only 0.4 egg each week during a half-month period, while a control group laid an average of 3.9 eggs each per week, or ten times as many in the corresponding period. This fluke may therefore cause severe losses to poultrymen.
45. *P. macrorchis* frequently occurs in hen's eggs.
46. This parasite is capable of causing pathological conditions in laying hens.
47. This fluke would not develop in resting oviducts.
48. The symptoms of prosthogonimiasis are discussed.
49. In prosthogonimiasis, as caused by *P. macrorchis,* there was found to occur a considerable plasma-cell infiltration into the oviduct tissue.

50. Positive diagnosis of prosthogonimiasis may be made through the finding of the eggs of *Prosthogonimus* by fecal examination, but negative results of such examination, even when concentration methods were used, were found to be unreliable.
51. To prevent their infestation with *Prosthogonimus,* it is necessary to keep hens fenced away from the shores of lakes containing the dragonfly intermediate hosts of the fluke.

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EXPLANATION TO LETTERING ON PLATES

a. mus.,	abortive muscle
cc.,	cyst cavity
cg.,	cuticular gland cell
cgr.,	cuticular groove
cgs.,	cuticular spine
cm.,	circular muscle
cp.,	cirrus pouch (sac)
cut.,	cuticula
dc.,	developing cercaria
ev.,	excretory vesicle
fib.,	muscle fibril
gb.,	germ ball
in.,	intestinal ceca
Lc.,	Laurer's canal
lm.,	longitudinal muscle
lum.,	lumen
mb.,	muscle band around cyst
mbo.,	inter-fibrillar lines
me., mem.,	membrane
Mg.,	Mehlis' gland
mus.,	muscle
nga.,	nerve ganglion
oes.,	oesophagus
oo.,	oötype
os.,	oral sucker
ov.,	ovary
ovid.,	oviduct
pc.,	parenchyma cell
pg.,	penetration gland
pha.,	pharynx
rf.,	radial fibril
sec.,	secretion layer
sr.,	seminal receptacle
tb.,	tail-bud of cercaria
te.,	testis
tp.,	primordium of testis
ut.,	uterus
vs.,	ventral sucker
yd.,	yolk duct

Unless otherwise specified, all drawings were made with aid of camera lucida. All figures on Plates II, III, and IV were traced from originals.

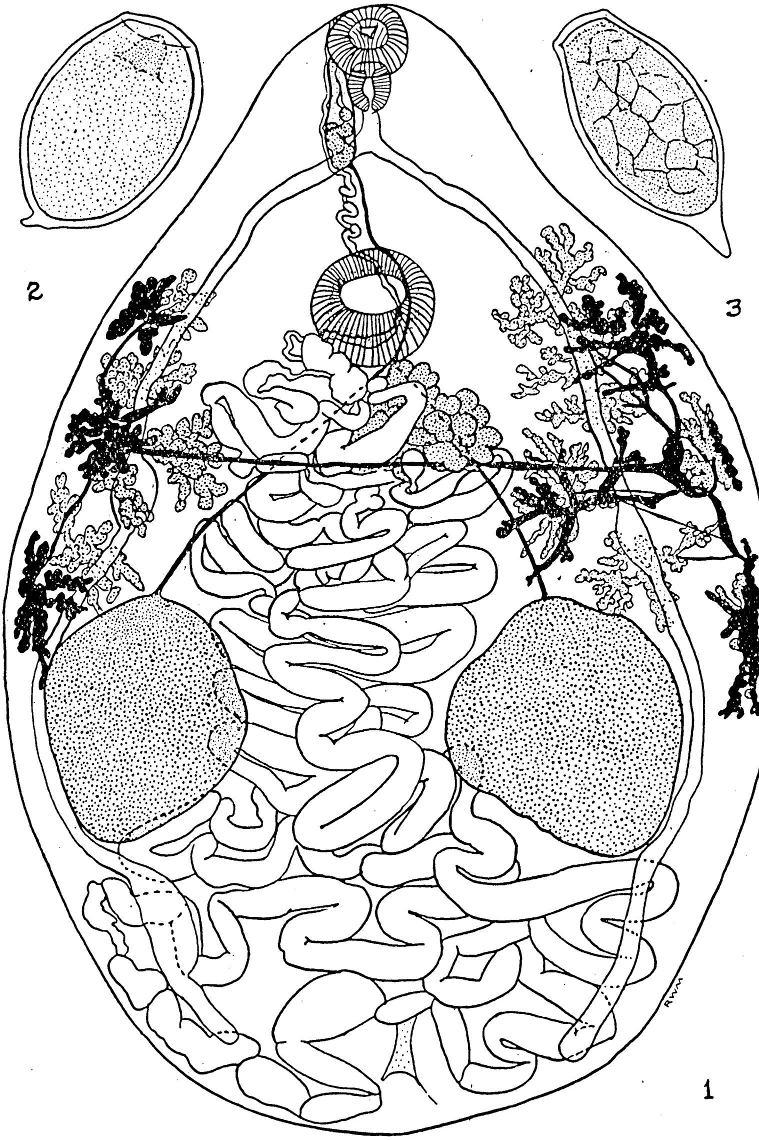
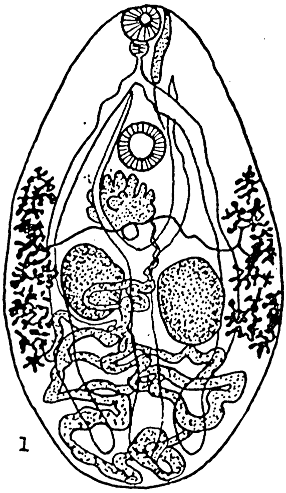


PLATE I

Fig. 1. *Prosthogonimus macrorchis,* type, dorsal aspect. Fig. 2. *P. macrorchis,* mature egg, showing normal spine. Fig. 3. *P. macrorchis,* segmenting egg, showing abnormal spine.

All drawn with the aid of camera lucida.



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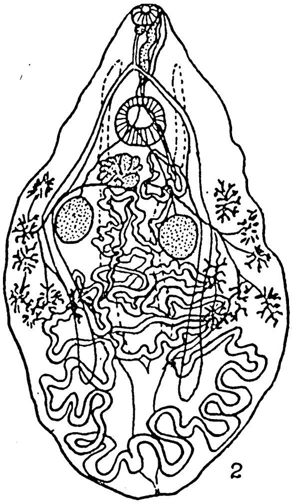

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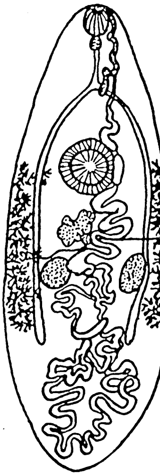

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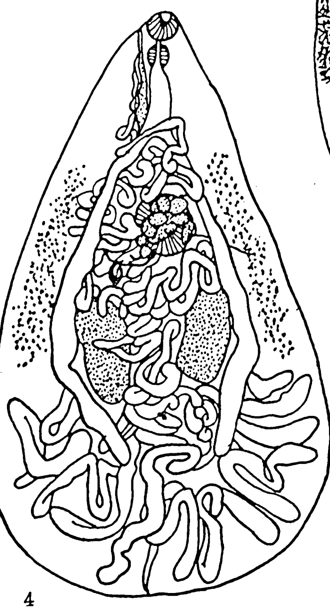

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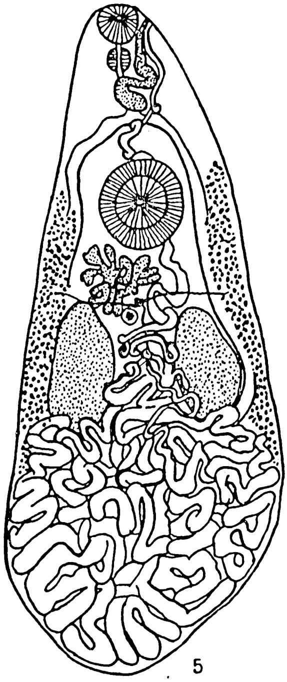

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Plate II

Fig. 1. *Prosthogonimus pellucidus* v. Linstow (after Szidat, 1926). Fig. 2. *P. horiuchii* Morishita and Tsuch (after Morishita, 1929). Fig. 3. *P. rudolphii* Skrjabin (after Skrjabin, 1923). Fig. 4. *P. ovatus* (Rudolphi) (after Braun, 1901a, ventral view of type). Fig. 5. *P. cuneatus* (Rudolphi) (after Braun, 1901a, dorsal view, from collect. of von Linstow).

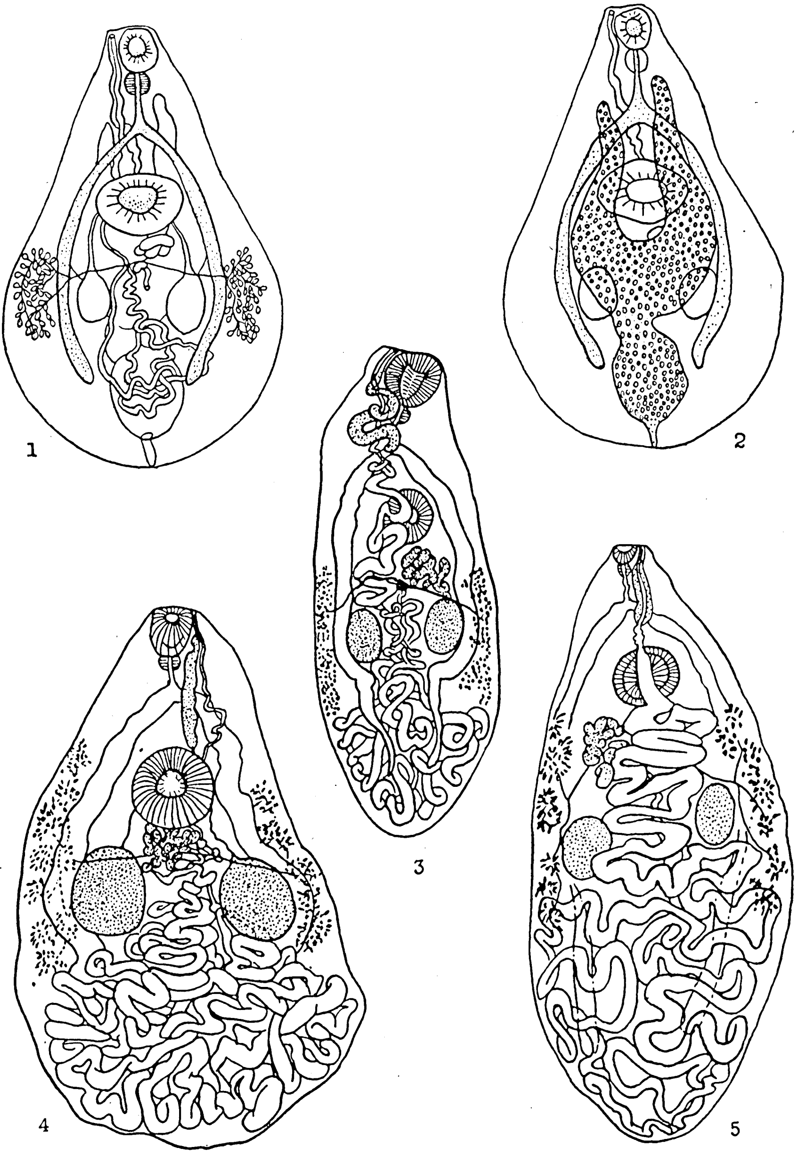

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PLATE III

Fig. 1. *Prosthogonimus anatinus* Markow (after Markow, 1902). Fig. 2. *P. anatinus,* showing excretory bladder (after Markow, 1902). Fig. 3. *P. japonicus* Braun (after Braun, 1901a, ventral view of type). Fig. 4. *P. putschkowskii* Skrjabin (after Skrjabin, 1913). Fig. 5. *P. fuelleborni* Skrjabin and Massino (after Skrjabin and Massino, 1925).

PLATE IV

Fig. 1. *Prosthogonimus brauni* Skrjabin (after Skrjabin, 1923b). Fig. 2. *P. vitellatus* Nicoll (after Nicoll, 1914). Fig. 3. *P. karausiaki* Layman (after Layman, 1926). Fig. 4. *P. dogiele* Skrjabin (after Skrjabin, 1914). Fig. 5. *P. skrjabini* Zakharow, 1920 (after Skrjabin, 1923b).

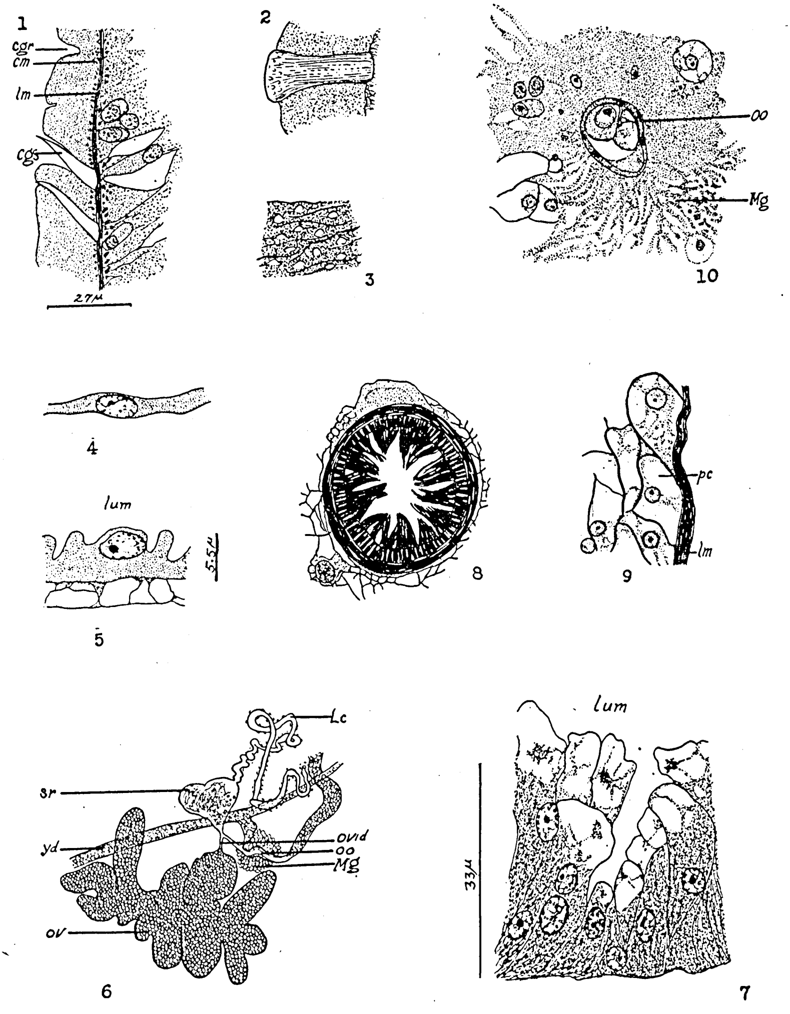

PLATE V. *Prosthogonimus macrorchis*

Fig. 1. Cuticula, near ventral sucker (long. sect.). Fig. 2. Cuticular spine, *in situ,* at posterior end of body. Fig. 3. Cuticula, showing spine arrangement (surface view). Fig. 4. Uterus, distended wall, (section). Fig. 5. Uterus, partially collapsed wall (section). Fig. 6. Oötype region, as seen in a small specimen. Fig. 7. Intestinal wall of columnar epithelium (cross sect.) Fig. 8. Laurer's canal, cross section. Fig. 9. Cirrus sac. part of section to show parenchyma cells. Fig. 10. Oötype, cross section.

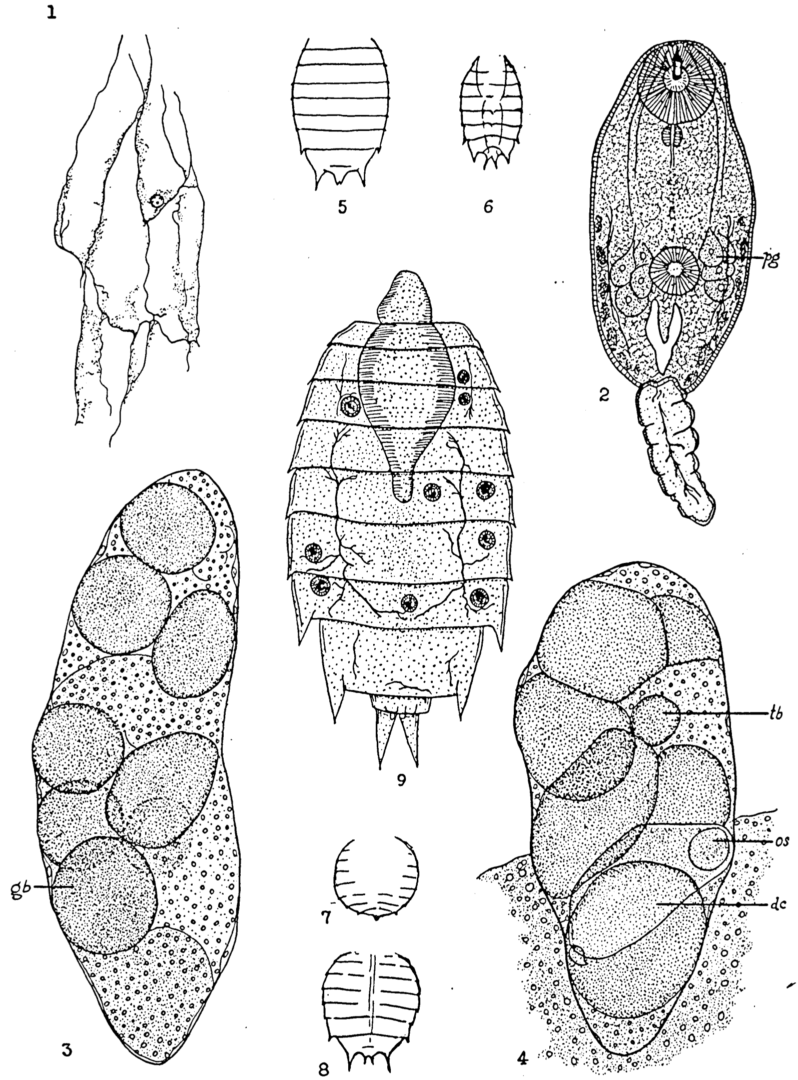

PLATE VI. *Prosthogonimus macrorchis*

Fig. 1. Parenchyma cells from mid-body region of adult (sect.) Fig. 2. Cercaria, from living specimens. Fig. 3. Sporocyst, from stained whole-mount. Fig. 4. Sporocyst, showing advanced stages of development of cercaria. Fig. 5. *Tetragoneuria* naiad, abdomen, (intermediate host). Fig. 6. *Leucorrhinia* naiad, abdomen, (intermediate host). Fig. 7. *Mesothemis* naiad, abdomen, (intermediate host). Fig. 8. *Epicordulia* naiad, abdomen, (intermediate host). Fig. 9. *Leucorrhinia,* naiad, abdomen cleared to show cysts of *Prosthogonimus macrorchis.*

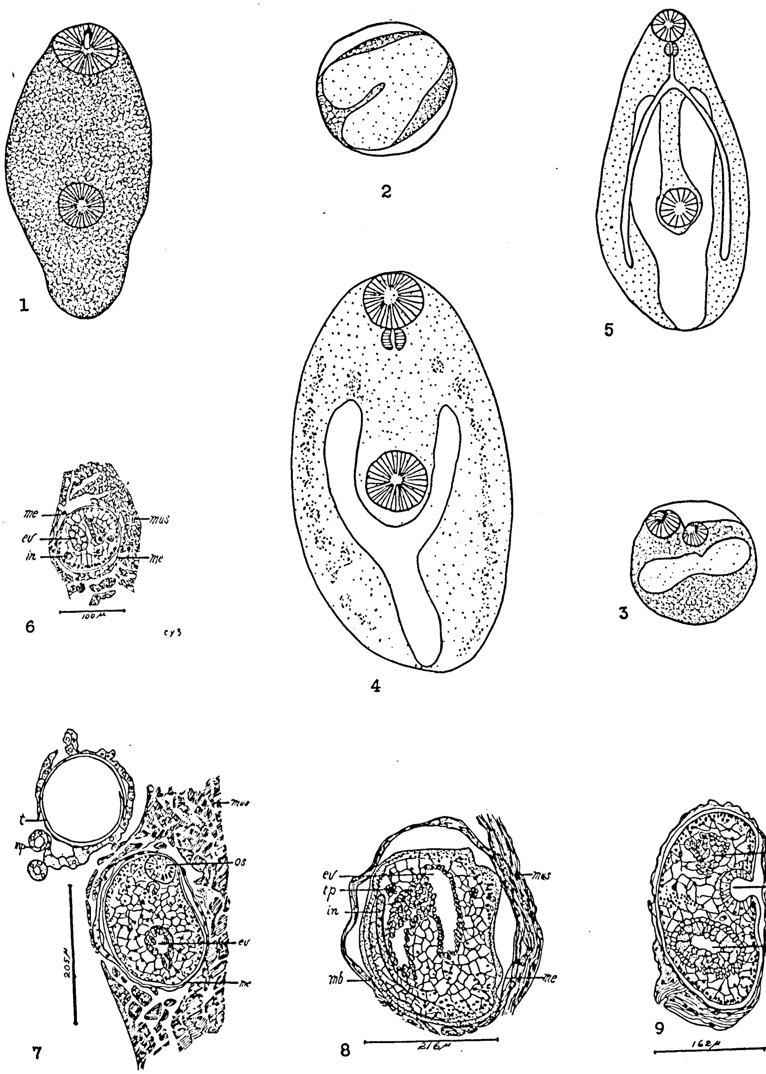

PLATE VII. *Prosthogonimus macrorchis*

Fig. 1. Metacercaria, 16 hours after entry into host. Fig. 2. Metacercaria, 21 days after entry into host. Fig. 3. Metacercaria, 21 days after entry into host (side view). Fig. 4. Metacercaria, 31 days after entry into host. Fig. 5. Metacercaria, 40 days after entry into host. Fig. 6. Metacercaria, in ventral abdominal muscle of dragonfly host (section). Fig. 7. Metacercaria, in ventral abdominal muscle of dragonfly host, later stage than Fig. 6 (section). Fig. 8. Metacercaria, in ventral abdominal muscle of dragonfly host, showing shape of excretory bladder and reproductive primordia (section). Fig. 9. Metacercaria, attached to edge of ventral abdominal muscle of host, just previous to formation of striated cyst wall.

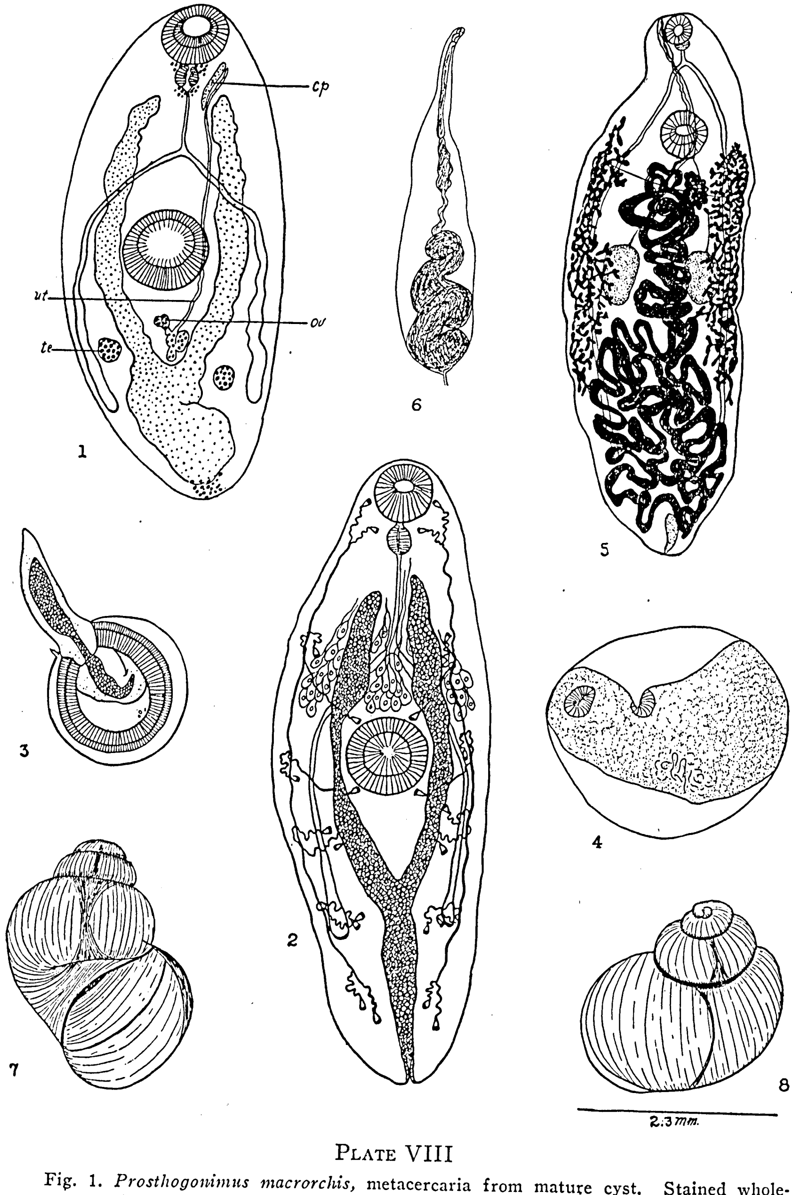

Plate VIII

Fig. 1. *Prosthogonimus macrorchis,* metacercaria from mature cyst. Stained wholemount, ventral view. Fig. 2. *P. macrorchis,* metacercaria from mature cyst showing especially the excretory system. From living specimens. Fig. 3. *P. macrorchis,* metacercaria escaping from cyst. Fig. 4. *P. macrorchis,* metacercaria, 27 days after entry into dragonfly intermediate host. Fig. 5. *P. rudolphii,* dorsal aspect. Collected by Dr. Wm. A. Riley, at Little Pelican Lake, Minnesota. From mallard duck. Fig. 6. *P. macrorchis,* cirrus sac. Fig. 7. *Amnicola limosa porata,* the first intermediate host of *P. macrorchis.* Fig. 8. *Amnicola limosa porata.*

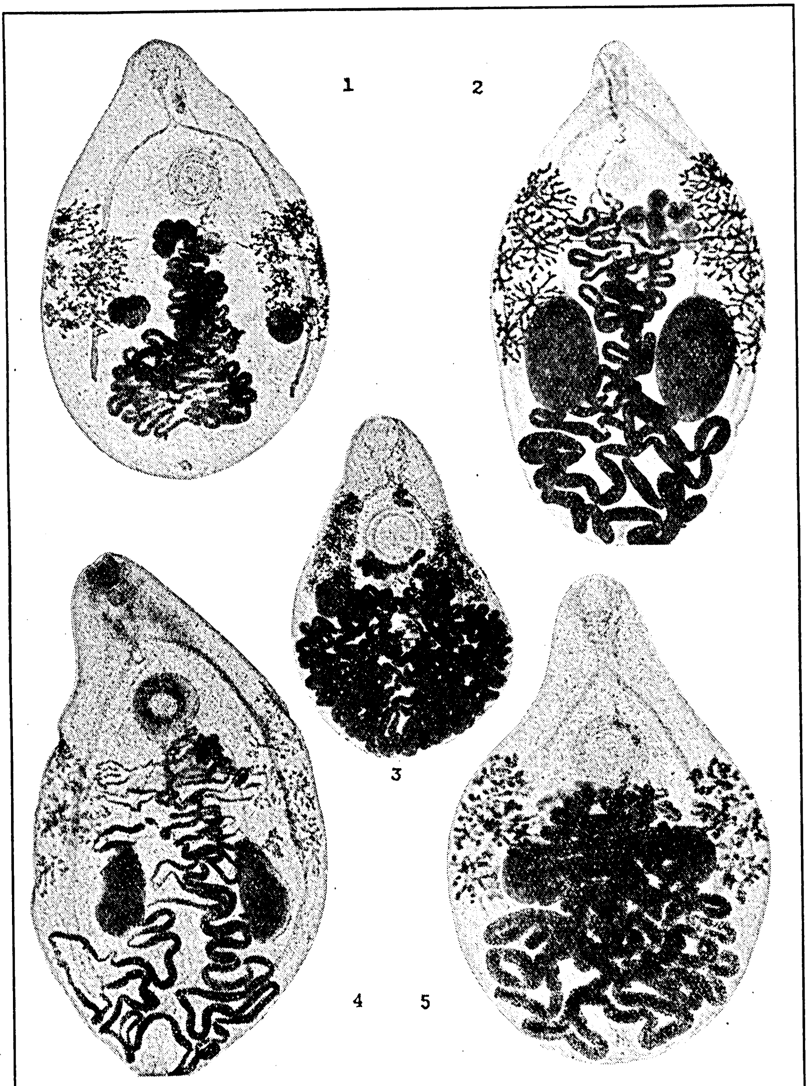

PLATE IX

Fig. 1. *Prosthogonimus macrorchis,* from bursa Fabricii of domestic duck. Fig. 2. *P. macrorchis,* from oviduct of domestic hen. Fig. 3. *P. macrorchis,* from bursa Fabricii of crow. Fig. 4. *P. macrorchis,* from oviduct of domestic duck. Fig. 5. *P. macrorchis,* from bursa Fabricii of English sparrow.

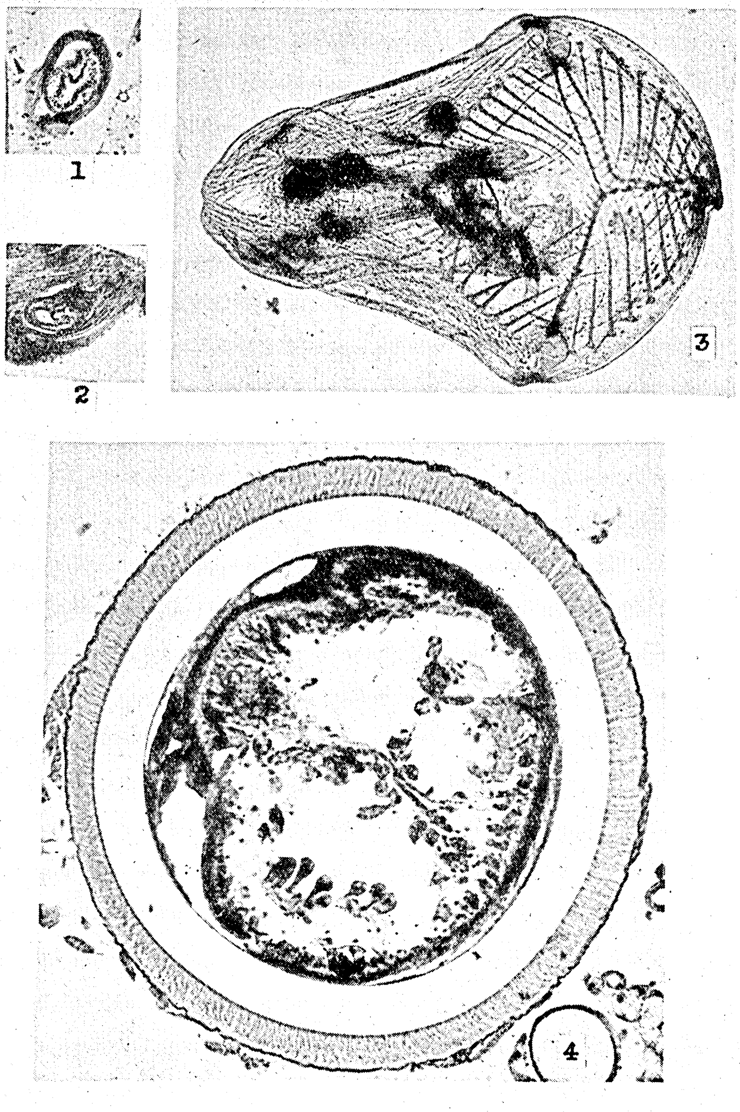

PLATE X

Figs. 1 and 2. Developing metacercaria of *Prosthogonimus macrorchis* in ventral thoracic muscles of *Leucorrhinia*. Fig. 3. Labium of *Leucorrhinia* containing three cysts of *P. macrorchis*. Fig. 4. Cyst of *P. macrorchis*, section in abdomen of *Leucorrhinia*.

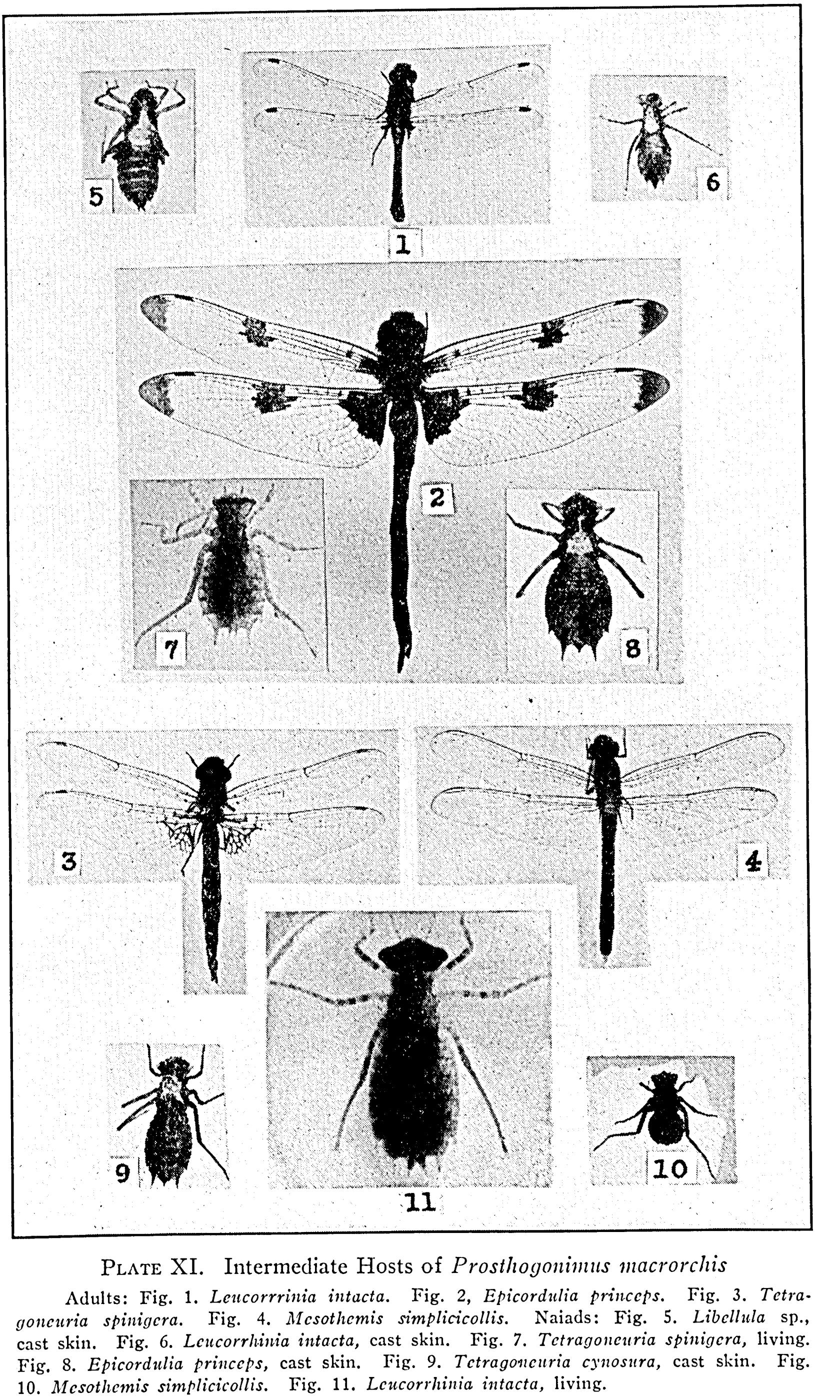

PLATE XI. Intermediate Hosts of *Prosthogonimus macrorchis*

Adults: Fig. 1. *Leucorrinia intacta.* Fig. 2, *Epicordulia princeps.* Fig. 3. *Tetragoneuria spinigera.* Fig. 4. *Mesothemis simplicicollis.* Naiads: Fig. 5. *Libellula* sp., cast skin. Fig. 6. *Leucorrhinia intacta,* cast skin. Fig. 7. *Tetragoneuria spinigera,* living. Fig. 8. *Epicordulia princeps,* cast skin. Fig. 9. *Tetragoneuria cynosura,* cast skin. Fig. 10. *Mesothemis simplicicollis.* Fig. 11. *Leucorrhinia intacta,* living.